NORTH AMERICAN FOSSIL ANGUID LIZARDS

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ABSTRACT

A survey of osteological and epidermal scalation characters of extant anguid lizards indicates that the Recent species fall into three groups worthy of subfamily status: (1) Gerrhonotinae (including Gerrhonotus, Abronia, and possibly Coloptychon), (2) Anguinae (including Ophisaurus and Anguis), (3) Diploglossinae (including Diploglossus, Wetmorena, and Ophiodes). Many characters were examined during this study, but the morphology of the frontal bones and body osteoscutes, presence or absence of a premaxillary foramen, and the participation of the postorbital in orbit formation are characters that have proved the most useful in both fossil and Recent forms.

Anguis is very close to Ophisaurus, differing from it only in features judged here to be degenerate. The ophisaurs are intermediate in many features between the Diploglossinae and the Gerrhonotinae, sharing with the former the unique premaxillary foramen and divided frontals, and with the latter a similar body scutellation. The anguines appear to be primitive in having toothed palatines and, in some species, toothed vomers.

Fossil remains unquestionably those of an anguid lizard first occur in late Cretaceous sediments of Wyoming and Montana. This anguid was first described by Gilmore (1928) as Peltosaurus? piger on the basis of two jaw elements. The generic assignment of this lizard was based on its having a tooth structure similar to that of the Oligocene Peltosaurus granulosus. A large number of previously unknown cranial elements recovered recently from the late Cretaceous Hell Creek Formation in Montana and from late Paleocene Bison Basin sediments in Wyoming indicates that this

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early anguid lizard is referable to *Pancelo-saurus,* n. gen., rather than to *Peltosaurus. Pancelosaurus piger* exhibits a mosaic of characters in its known skeletal parts and shows resemblance to the Recent anguids *Ophisaurus, Gerrhonotus,* and *Diploglossus.* Since the body osteoscutes of the Creta-ceous form most closely resemble those of *Gerrhonotus* and *Ophisaurus,* perhaps the extinct genus was already specialized toward the line leading to the latter two Recent genera. *Pancelosaurus piger* ex-hibits many of the same primitive and intermediate characters between the diplo-glossines and the gerrhonotines as do the ophisaurs, and it is regarded here as a primitive limbed member of the Anguinae. *P. piger* is known from the late Cretaceous through the late Paleocene and the genus extends into the middle Oligocene as *P. pawneensis* (formerly *Xestops pawneensis*).

The large Eocene and Oligocene fossil forms *Xestops, Peltosaurus, Melanosaurus, Glyptosaurus,* and *Arpadosaurus gazin-orum,* n. gen., n. sp., may also have been derived from *Pancelosaurus* or its relatives, as indicated by a similar type of body osteoscute. These are more robust than those of *P. piger,* are always covered with tubercular mounds, and are often laterally sutured. This sculpture type is found only in the above forms, and in combination with a characteristic pattern of labial suturing between dentary and postdentary bones, indicates the distinctiveness of this group, which is placed here in a subfamily Glyptosaurinae. In this concept of the glyptosaurines, the Eocene species *Xestops vagans* appears to be the most primitive form and shares some primitive features of the frontal bones with *P. piger* while ex-hibiting the above-mentioned glyptosaurine characters. *Dimetopisaurus wyomingensis* Hecht is a synonym of *Xestops vagans. Arpadosaurus* appears to be also referable to the Glyptosaurinae as constituted here, and is structurally intermediate between *Melanosaurus* and *Glyptosaurus.* It is postulated that *Glyptosaurus* may have

originated from a form like *Melanosaurus* through *Arpadosaurus,* but more evidence is needed to confirm this hypothesis, which is based on contemporaneous fossil genera. The glyptosaurines represent a side line of anguid evolution rather than being an-cestors of the modern forms.

INTRODUCTION

Until recently, detailed anatomical knowl-edge of the cranium of fossil anguids was based only on Eocene and Oligocene forms. Most of this descriptive anatomical work was carried out by Gilmore (1928, pp. 91–144; 1938, pp. 16–21). The presence of anguid remains in earlier deposits (Upper Cretaceous and Paleocene) was indicated by Gilmore (1928, pp. 136–138), and later by Gazin (1956, p. 12) and Estes (1964, pp. 119–125). The latter author gave a detailed description of the maxilla and dentary of this early anguid, but it was not until recently that most of the cranial elements of this form were identified among thousands of fragmentary bones of other species from late Cretaceous Hell Creek Formation sites near Fort Peck Reservoir, McCone Co., Montana (Sloan and Van Valen, 1965). This large amount of fossil matrix was obtained through the method of screening and washing as de-scribed by McKenna (1962) and sorted for faunal studies now in progress by Estes, Berberian, and Meszoely (1969) (studies similar to that of Estes, 1964). These new finds not only gave us a more detailed knowledge of the cranial anatomy of this earliest known anguid, but also yielded information about the epidermal scalation.

In an attempt to shed new light on the evolution and interrelationships of the fossil and recent members of the Anguidae, the earliest well-known anguid, "*Pelto-saurus*" *piger,* is described here in detail and its cranial elements are compared with those of Recent and fossil forms. It is re-ferred below to *Pancelosaurus,* n. gen. Well over one hundred Recent skeletons, hun-dreds of fragmentary remains of *P. piger,*

and a great number of other fossil specimens, including the holotypes of most North American anguid species, have been examined. This study has resulted in reclassification of both modern and extinct anguids and has provided information on several phyletic lines within the Anguidae.

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Abbreviations used here are as follows:

AMNH   American Museum of Natural History, New York, N. Y.

BM(NH)   British Museum (Natural History), London, England

CM   Carnegie Museum, Pittsburgh, Pa.

FAM   Frick collection at the American Museum of Natural History, New York, N. Y.

FMNH   Field Museum of Natural History, Chicago, Ill.

KU   Museum of Natural History, University of Kansas, Lawrence, Kan.

MCZ   Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

PU   Princeton University Museum, Princeton University, Princeton, N. J.

UC   Museum of Paleontology, University of California, Berkeley, Calif.

USNM   United States National Museum, Washington, D. C.

YPM   Peabody Museum of Natural History, Yale University, New Haven, Conn.

REVIEW OF CLASSIFICATION

Families and Subfamilies

The family Anguidae was erected by Cope (1864, pp. 227–228) for lizards earlier grouped, on the basis of external characters, either with the Scincidae (*Diploglossus* and related genera) or with the Zonuridae (*Ophisaurus* and *Anguis*). In this first revision of the Diploglossa, Cope did not include the gerrhonotines in the family Anguidae, but granted them family rank as the Gerrhonotidae. The main criterion for Cope's action was the absence of a premaxillary foramen (located on the palatal junction of premaxilla and maxilla) in the gerrhonotines that was present in the other members of the Anguidae. He further subdivided his family Anguidae into four subfamilies on the basis of characters of the interclavicle (mesosternum of Cope) and the presence or absence of a lateral fold. The subfamilies were as follows:

(1) Diploglossinae, with no lateral fold and with elongated limbs of the interclavicle; including the South American *Diploglossus* and related forms. (2) Anguinae, with no lateral fold and with shortened interclavicle; only *Anguis fragilis* is included here. (3) Ophisaurinae, with a lateral fold and with interclavicle reduced or missing. Cope included here, along with the ophisaurs, the South American *Ophiodes* (=*Opheodes*), now included in the Diploglossinae. (4) Opheomorinae, without lateral fold (no character for the interclavicle given), contained only a single genus, *Opheomorus*, a name now applied to a group of African skinks.

Boulenger (1883, pp. 119–120) accepted Cope's conclusions in general, but listed no subfamilies and included the gerrhono-

tines in the family Anguidae. In 1885 he repeated the same classification, but described the anatomical characteristics of the family in more detail.

Cope (1900, pp. 488–492), influenced by Boulenger, included the gerrhonotines in the family Anguidae as one of the four subfamilies, and omitted the questionable Opheomorinae included among his earlier subfamilies. It is interesting to note that he here included *Ophiodes* in both Ophisaurinae and Anguinae (to neither of which this form belongs). Characters used for subdivision of the family were essentially the same as those utilized in the 1864 revision.

Camp (1923) did not go below the family level in his classification of lizards, but in considering a given family he referred to representative genera or species and to the relationship of these forms to one another within the family. His findings, especially with respect to the throat musculature, appear to support a close relationship between the ophisaurs and *Anguis.* "The Anniellidae are close to *Gerrhonotus* in structure of throat musculature and hemipenis. *Ophiodes* resembles *Celestus* in the former respect. *Gerrhonotus* and *Ophisaurus* are not as closely related as the latter is to *Anguis*" (Camp, 1923, p. 418; see also p. 373). Camp (1923, p. 340) also noted the resemblances between the hyoids of *Anguis* and *Ophisaurus*, in both of which (alone among anguids) all traces of the third arch are lost.

Camp (1923, pp. 327–329) also attempted to include fossil anguids in his classification and grouped them all, with the exception of the European fossil ophisaurs, in the extinct family Glyptosauridae of Marsh (1872). In this family he recognized four North American genera: *Xestops, Peltosaurus, Glyptosaurus, Helodermoides,* and questionably the European *Placosaurus.* Camp believed these fossils to represent an homogenous group, somewhat intermediate between the families Anguidae and Helo-

dermatidae. He listed twelve characters in which the glyptosaurids differ from the former family, and twelve more characters in which they differ from the latter.

His characters separating the Glyptosauridae from the Helodermatidae are reprinted here (Camp, 1923, p. 328):

1. Presence of a supratemporal arch and fenestra
2. Separation of prefrontal and postfrontal above orbit
3. Postfrontal and postorbital entirely distinct
4. Pediculate caudal chevrons on the centra
5. A pineal foramen (very small in *Xestops,* absent in *Peltosaurus*)
6. Imbricated osteoderms on the body
7. Teeth on the pterygoid, palatine and prevomerine bones
8. Parietal united by suture (fused in *Peltosaurus*)
9. Transverse process of first caudal vertebra arising from the entire length of the centrum as in *Gerrhonotus*
10. Jugal with angular process
11. Frontals fused (separate in *Helodermoides*)
12. Teeth highly pleurodont with cylindrical, solid shafts and blunt, highly wrinkled crowns, as in some Anguidae.

Camp remarked that with the exception of unfused parietals, the above characters would allow the fossil forms to be included in the family Anguidae (in which he grouped the recent forms). Neither Gilmore (1928, p. 93) nor I found any trace of parietal suture in any Recent or fossil anguid (including Camp's Glyptosauridae). In addition, a parietal foramen is present in all fossil forms in which this region is preserved.

Camp's characters separating the Glyptosauridae and Anguidae are given as follows (Camp, 1923, p. 328):

1. The great extent of the patches of teeth on the pterygoid and palatines
2. The massive rectangular jugal, somewhat as in *Heloderma*
3. The extremely large tabulare, exposed dorsally as in *Heloderma*
4. The great length of the slender squamosal which extends forward nearly to the jugal
5. The corresponding reduction of the postorbital
6. The embossed tuberculate osteoderms slightly suggesting *Heloderma* in ornamentation
7. Quadrate peculiar in having a broad, thin, semicircular internal wing
8. Lower jaw massive; curved posteriorly as in *Heloderma*
9. Meckelian sulcus completely covered
10. Splenial extensive posteriorly
11. Angular with extensive external surface covering the surangular as a thin plate, somewhat as in *Gerrhonotus*
12. Paroccipital a separate element

Gilmore (1928, p. 93) dismissed Camp's reasons for not including the fossils in the family Anguidae as characters correlated with the large size of the fossils (points 2, 8), as applicable to some fossils only (1, 3, 7), as also present in the Recent forms (9, 10, 11), and the remaining as not of family significance. I believe that a number of Camp's glyptosaurid characters (e. g., 1, 3, 7, 12) were based on specimen AMNH 5168, and are not necessarily present or determinable in other fossils. This specimen was restored by Camp as *Xestops* and later was referred to a new genus *Melanosaurus* by Gilmore (1928, p. 138).

Kuhn (1940) gave a classification that resulted from a study on Middle Eocene anguids from Geiseltal, Germany. Kuhn distributed these fossil forms into two families in which he believed that two different trends existed. In one line, the Anguidae, a tendency toward limb reduction and body elongation occurred, as well as a tendency toward thinner osteoscutes. He recognized the following fossil and Recent forms as Anguidae: *Propseudopus, Pseudopus* (= *Ophisaurus*), *Eurosaurus, Anguis, Diploglossus, Melanosauroides, Ophipseudopus, Parapseudopus,* and *Ophisauriscus*.

In the other line, the Placosauridae, Kuhn saw no tendency toward limb reduction; the body is relatively short and the osteoscutes have well-developed tubercular sculpture. Here he includes: *Placosaurus, Glyptosaurus, Peltosaurus, Melanosaurus, Xestops, Placosauriops, Placosauroides,* and *Placotherium*. All members of this family are fossil.

McDowell and Bogert (1954) divided Recent and fossil members of the family Anguidae into four subfamilies: (1) Glyptosaurinae, (2) Gerrhonotinae, (3) Diploglossinae, and (4) Anguinae. Their conclusions regarding major characteristics of subfamilies and forms comprising these subfamilies are recapitulated below.

(1) The fossil Glyptosaurinae are the only anguids in which the following characters are exhibited: irregularly arranged and polygonal head osteoscutes, extremely large body size, and frontals widened in the interorbital region. This subfamily includes the North American genus *Glyptosaurus,* and the European *Placosaurus* and *Placotherium*. The first two generic names are probably synonymous.

(2) The Gerrhonotinae include *Gerrhonotus, Abronia, Coloptychon, Ophisaurus,* the fossil *Peltosaurus,* and perhaps also Kuhn's (1940) *Placosauriops* and *Placosauroides*. Members of this subfamily have rectangular scutes overlapping anteroposteriorly but sutured laterally, and an unossified fold is present between ventral and dorsal armor.

(3) In the Diploglossinae, no lateral fold is present, and there is no suturing between osteoscutes. The latter overlap laterally as well as anteroposteriorly, and conse-

quently the lateral surfaces are also beveled. The subfamily includes the Central and South American Recent anguids and the fossil *Xestops*.

(4) In the Anguinae, the single genus *Anguis* resembles the Diploglossinae in the above respects, but is distinguished from them in having fanglike dentition and a palate in which the anterior border of the palatine is in front of both the posterior extremity of the vomer and the anterior end of the interpterygoid vacuity.

Hoffstetter (1962a) examined osteoscutes of fossil and Recent anguids and concluded that on the basis of similar scutes and absence of lateral fold, the Anguinae and the Diploglossinae possibly should be combined in a single subfamily. Hoffstetter recognized only one other subfamily in the Anguidae, the Gerrhonotinae, in which he grouped Recent limbed gerrhonotines and ophisaurs and all extinct anguid genera. Hoffstetter listed the following fossil forms under the subfamily Gerrhonotinae: *Peltosaurus*, *Placosauriops*, *Placosauroides*, *Melanosaurus*, *Placosaurus*, *Glyptosaurus*, *Propseudopus*, *Parapseudopus*, *Ophipseudopus*, *Ophisauriscus*, and *Xestops*. He argued that all these forms exhibit the same type of robust, well-ossified, rectangular osteoscutes with well-developed gliding surfaces, and that these scutes may be sutured, beveled, or a combination of both along their lateral border.

The preceding historical treatment of anguid classification may be summarized as follows:

1. Since Cope's second classification (1900) there has been no disagreement as to what Recent forms belong in the family Anguidae.
2. In the three major attempts to divide the family into subfamilies (Cope, 1900; McDowell and Bogert, 1954; and Hoffstetter, 1962a), body scutellation and the presence or absence of a lateral fold have been heavily relied upon, especially by the latter two authors.
3. On two occasions (Camp, 1923; Kuhn, 1940) the large Eocene and Oligocene forms were considered an homogenous group and transferred from the Anguidae into a separate family (Camp's Glyptosauridae and Kuhn's Placosauridae).

Recent Genera and Subgenera

Tihen (1949) examined skull structure and scutellation in the limbed gerrhonotines, and on the basis of these characters recognized five genera within this group: *Coloptychon*, *Abronia*, *Gerrhonotus*, *Elgaria*, and *Barisia*. He also supported the inclusion of the fossil *Melanosaurus* and *Peltosaurus* in the subfamily Gerrhonotinae.

Stebbins (1958) described a new species of alligator lizard, *Gerrhonotus panamintinus*. In order to determine the taxonomic position of the new lizard, Stebbins re-examined Tihen's genera. He found that the *Elgaria-Gerrhonotus* group is generally oviparous and the *Barisia* group ovoviviparous. However, *Elgaria coerulea* is ovoviviparous, and this form exhibits a number of characters (scutellation, pigmentation, and number of pterygoid teeth) intermediate between the genera *Barisia* and *Elgaria*. In view of the intergradation among the above genera, Stebbins proposed to group three of Tihen's genera (*Elgaria*, *Gerrhonotus*, and *Barisia*) into a single genus *Gerrhonotus* with two subgenera, *Barisia* and *Gerrhonotus* (the latter including *G. liocephalus* and members of the genus *Elgaria*). Stebbins regarded the characters given by Tihen as insufficient for generic (or even subgeneric) separation of *Elgaria* and *Gerrhonotus* and referred them both to the subgenus *Gerrhonotus*. Bogert and Parker (1967) considered *Barisia* a genus for purposes of their discussion. Criley (1968) examined osteological characters of gerrhonotiform lizards and concluded that it is impossible to support *Barisia* and *Elgaria* on an osteological basis, either as genera or as subgenera.
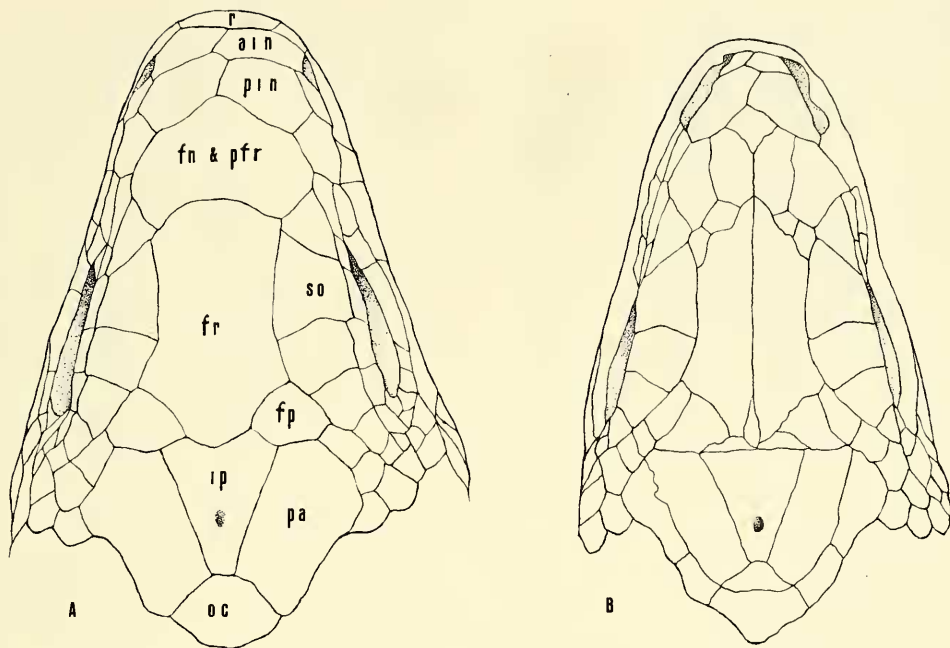
Figure 1. Lack of correspondence between cranial osteoscutes and epidermal scales: A, head of *Diploglossus hewardii,* MCZ 45170, Recent, with epidermal scales; B, the same with epidermal scales removed, exposing osteoscutes; both × 4. The skull in B is shrunken because of desiccation. For abbreviation see p. 147.

McConkey (1954) examined North American members of the genus *Ophisaurus* and recognized three distinct species on the basis of scutellation and ratio of body to tail length: *O. ventralis, O. compressus,* and *O. attenuatus.* In the last he distinguished two subspecies, *attenuatus* and *longicaudus.* McConkey later (1955) described a new species, *O. incomptus,* from Mexico. Holman (1965) added another new species, *O. ceroni,* also from Mexico. Five other species of *Ophisaurus* are known from Eurasia and Africa: *O. apodus, O. buttikoferi, O. gracilis, O. harti,* and *O. koellikeri.*

Underwood (1959) revised the subfamily Diploglossinae, members of which occur in South America and the West Indian Islands. In the past, South American forms had been placed in the genus *Diploglossus,* whereas island forms were referred to the genus *Celestus.* The criterion of distinction used by Burt and Burt (1931) was the presence of claw sheaths and three prefrontal epidermal scales (1 frontonasal and 2 prefrontals of this paper, Fig. 1) in the former; no claw sheaths and a single prefrontal in the latter. Underwood found overlap in both these characters; three island forms have a claw sheath (*D. delasagra, D. pleeii,* and *D. microblepharis*), and *D.* (=*Sauresia*) *sepsoides* and *D. darlingtoni* occasionally have 3 prefrontals. Therefore he regarded both *Celestus* and *Sauresia* as members of the genus *Diploglossus.* Underwood (1964) described a new species, *Diploglossus montiserrati,* from the Leeward Islands. This lizard resembles the "typical" mainland forms (especially *D. monotropis*), thus further tending to de-emphasize the distinctions between island and mainland forms.

In this paper, I shall use the generic classification of Stebbins (1958), McConkey (1954), and Underwood (1959) for the Recent anguids.

DESCRIPTION OF RECENT ANGUID GENERA

Anguids do not contribute extensively to the present-day herpetological fauna either in number of individuals or in number of species. There are approximately 62 species of Recent anguids recognized currently, distributed among seven genera. The family contains arboreal forms (members of the genus *Abronia*) and limbless semi-burrowers (*Ophisaurus, Anguis,* and *Ophiodes*); the rest of the genera are terrestrial. Anguids at present occur in Palearctic, Nearctic, Neotropical, and Oriental geographical realms, with only limbless forms in the Old World continents, and only one genus, *Ophisaurus,* occurring both in the Old and the New World.

Living anguid genera fall into four general groupings: (1) the North and Central American *Gerrhonotus* and *Abronia,* (2) the North American and Eurasian ophisaurs, (3) the European monotypic *Anguis,* and (4) the South and Central American *Diploglossus, Wetmorena,* and *Ophiodes.* These four groups correspond essentially to Cope's (1900) subfamilies, with *Ophiodes* is placed in the diploglossines. Consideration of each of these groups as a unit facilitates discussion of the distribution of osteological and scutellation character-states among Recent anguids; a subfamilial classification will follow the discussion of fossil genera.

Anguis fragilis

Osteological material. (3) *Anguis fragilis,* MCZ 1032, 3958, 37174.

Skull: Teeth with unstriated crowns, recurved, fanglike, and widely spaced; five to seven teeth in each maxilla and dentary; palatal bones edentulous pterygoids; slender, widely separated from one another at the midline, and with elongated palatine processes (measuring one-third of the total length of the pterygoid); premaxillary foramina present at union of premaxilla and maxilla (Fig. 2c). Frontals not fused, orbital borders almost straight and not in contact with maxilla; olfactory process of frontal not in contact with dorsal process of palatine; body of parietal and frontal of approximately equal length; parietal foramen present; postfrontal and postorbital distinct, with postorbital excluded from the orbit; jugal with only a suggestion of a posterior process. Surangular and articular unfused, with surangular extending well beyond well-developed anterior process of coronoid on the labial surface of the dentary (Fig. 3a); dentary not in contact with anterior supra-angular foramen; both dentary and splenial participate in formation of anterior inferior alveolar foramen (Fig. 4a).

Vertebrae: 62 presacrals (not including atlas and axis), 61 with ribs and first four with ventromedial hypapophysial processes; single sacral; first caudals with hemal arch bases indistinguishably fused to centra; ribs with tubera costarum.

Individual presacral vertebrae procoelous, elongate, flattened ventrally with prominent paired subcentral foramina; lateral margins slightly concave in ventral view (Fig. 5d). Condyles large, flattened ventrally, slightly exceeding breadth of centrum immediately before condyle; condylar head with little ventral exposure. Neural spines moderately low with weblike process on leading edge of spine. Single sacral with forked, lobsterclaw-shaped transverse process slightly curved posteriad; anterior prong of fork distally much larger than posterior.

Caudals less concave than presacrals, with relatively narrower centra and chevrons indistinguishably fused to centra. Bases of transverse processes often bifurcate and the autotomy plane well marked, extending across vertebra in an arch between the bases of transverse processes.

Epidermal scalation: Frontonasal and frontal in narrow contact; frontal and interparietal in very broad contact, widely separating the small frontoparietals; interparietal large and in narrow contact with small occipital.
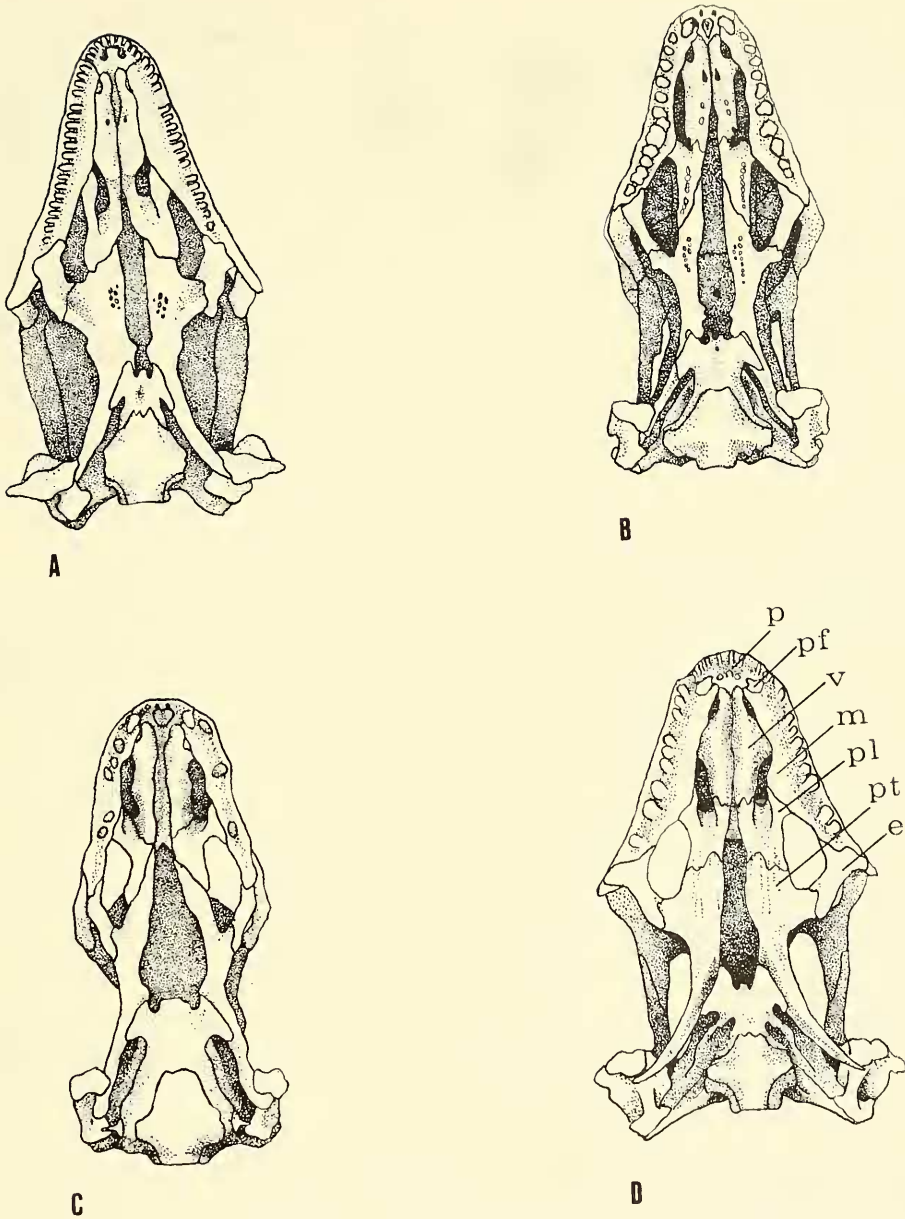
Figure 2. Skulls of recent anguids in ventral view: A, *Gerrhonotus liocephalus*, MCZ 19062; B, *Ophisaurus apodus*, MCZ 2094a; C, *Anguis fragilis*, MCZ 37174; D, *Diploglossus occiduus*, BM(NH) 63.2.21.17. Note presence of large premoxillary foramen in all except *Gerrhonotus*, at junction of premaxilla with maxilla. A × 2, B × 1.5, C × 4 and D × 1.25. For abbreviations see p. 147.

Body scales unkeeled, smooth; *in situ* wider than long; no lateral fold.

Body osteoscutes: Thin with rounded outlines; middorsals almost round with halfmoon-shaped, lateroposteriorly-recurved gliding surfaces (Fig. 6c). Laterals elliptical with gliding surface extending along almost entire left or right edge of osteo-
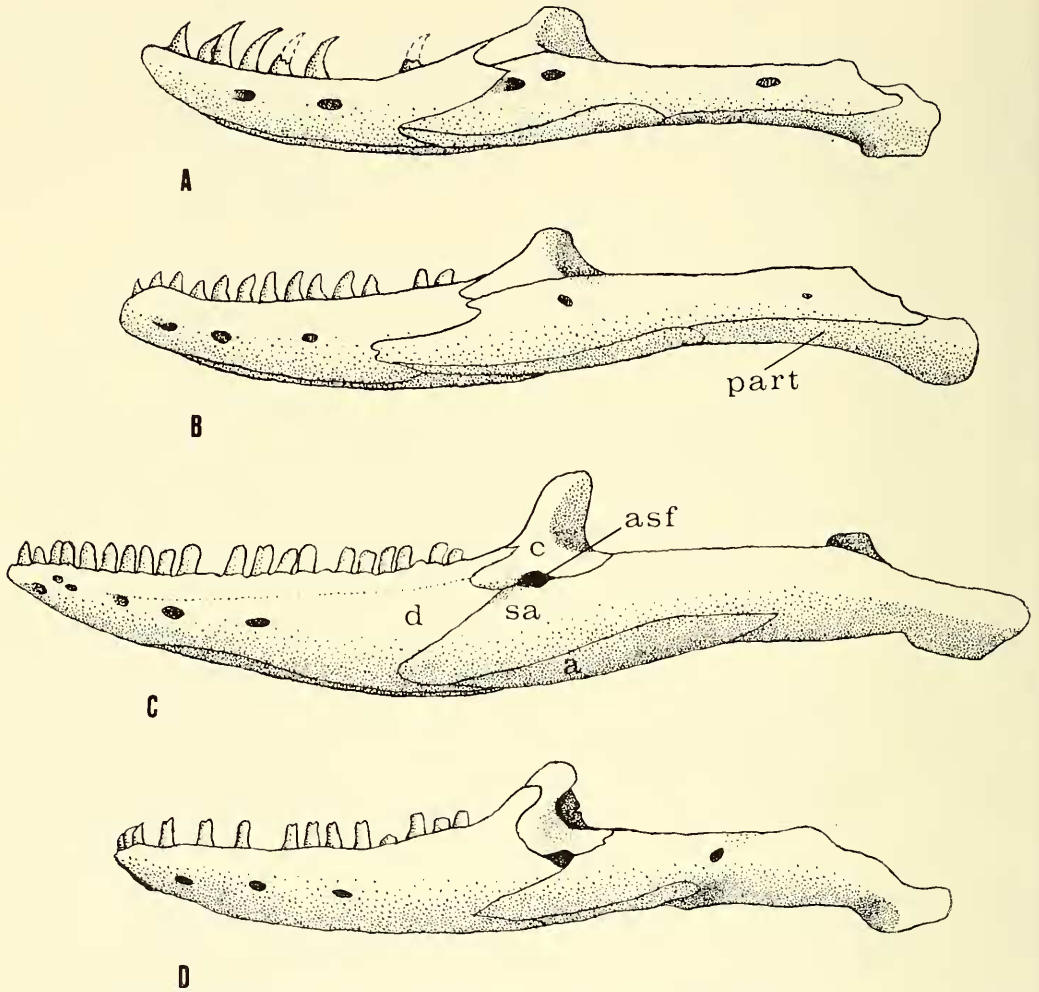
Figure 3. Mandibles of recent anguids in labial view: A, *Anguis fragilis*, MCZ 37174; B, *Ophisaurus gracilis*, MCZ 15836; C, *Gerrhonotus (Barisia) imbricatus imbricatus*, MCZ 97400; D, *Diploglossus barbouri*, MCZ 7367a. Note resemblance between A and B and also note that in all forms surangular exceeds coronoid anteriorly. All × 6. For abbreviations see p. 147.

scute (depending on side of origin) and becoming confluent with lateral bevel. Midventrals with greatest width along the gliding surface, becoming narrower posteriorly.

Ophisaurus

Osteological material. (4) *Ophisaurus apodus,* MCZ 32249, 2094, AMNH 75481, 73228; (2) *O. attenuatus,* MCZ 5548a-b; (1) *O. compressus,* MCZ 12825; (1) *O.*

gracilis, MCZ 15836; (1) *O. harti,* MCZ 46916; (1) *O. koellikeri,* MCZ 61138; (4) *O. ventralis,* MCZ 620, 32258, 55509, 1949.

Skull: Teeth ranging from blunt-crowned, robust crushing teeth in *Ophisaurus apodus* to recurved, widely-spaced, fanglike types with pointed apices and unstriated crowns in *O. harti.* Teeth in general more pointed and less chisel-shaped (especially in the Old World forms) than in *Gerrhonotus* or *Diploglossus* and allies; palatal teeth pres-

ent on pterygoid and palatine on all examined species. Auffenberg (1955, p. 133) indicates that teeth are absent from the palatine bone in *O. attenuatus;* in both MCZ specimens of *O. attenuatus attenuatus* available to me, however, teeth were present on the palatine bone (Fig. 2b). In *Ophisaurus apodus* teeth also present on vomers; palatine teeth arranged either in rows or patches; pterygoids slender, widely separated, with elongated palatine processes (measuring at least one-third of total length of pterygoid). Premaxillary foramina present; frontals unfused, with almost straight orbital borders, not in contact with maxilla; olfactory process of frontal not in contact with dorsal process of palatine except in *O. gracilis;* parietal foramen present; postorbitals and postfrontals distinct, with postorbital excluded from orbit; surangular and articular distinct in *Ophisaurus apodus* and *O. harti;* surangular well in advance of the anterior coronoid process; anterior labial process of coronoid well developed (except in *Ophisaurus apodus,* in which backward extension of dentary prevents development of this process, paralleling the situation noted for *Diploglossus* and related forms). Both dentary and splenial involved in formation of anterior inferior alveolar foramen (Fig. 4d). Anterior supra-angular foramen labially placed, not in contact with dentary (Fig. 3b).

Vertebrae: Presacrals (not including atlas and axis) in the mid-fifties, excepting *Ophisaurus compressus* with 44; only available counts, *O. apodus* (52–53), *O. attenuatus attenuatus* (56–57), *O. a. longicaudus* (54), *O. harti* (55), *O. ventralis* (57). Single sacral; first caudal with hemal arch bases indistinguishably fused to centra. Ribs with tubera costarum.

Individual presacral vertebrae ventrally flattened with paired subcentral foramina (Fig. 5c); neural spine angles made with centrum more acute than in *Anguis fragilis;* anterior weblike extension on leading edge of spine little developed. Condyle large with little ventral exposure. Single sacral with bifurcated, posteriad-directed, lobsterclaw-like transverse process as in *Anguis.* Caudal chevrons indistinguishably fused to centra.

Epidermal scalation: Frontonasal and frontal contact variable in the genus; the above scales in narrow contact in *Ophisaurus apodus, O. gracilis,* and *O. ventralis* (variation probably occurs in all forms, as noted by McConkey, 1954, pp. 142, 147, 150; tables 1a, 2a, 3a); no frontal contact in *O. attenuatus, O. ceroni* (from Holman, 1965) or *O. buttikoferi;* contact highly variable in *O. harti;* in two small *O. koellikeri* frontonasal fused with the two lateral prefrontals, in a single large specimen frontonasal distinct and in contact with frontal. In all, contact is wide between frontal and interparietal, and consequently the small interparietals are widely separated. Interparietal large and in narrow contact with small occipital.

Body scales wider than long, keeled in *Ophisaurus apodus, O. attenuatus, O. ceroni* (from Holman, 1965), *O. harti, O. koellikeri, O. ventralis;* lateral fold present in all.

Body osteoscutes: Much thicker than in *Anguis* and more angular (Fig. 6b). Lateral osteoscutes with bevel along their lateral edges; gliding surface occupying less than one-half total length of scute and with appearance of a transverse band; middorsals fanned out posteriad, with bevels along both lateral surfaces; midventrals wedge-shaped, with less prominent bevels along ventrolateral edges.

Gerrhonotus and Abronia

Osteological material. (1) *Abronia deppii,* MCZ unnumbered specimen. (1) *Gerrhonotus coeruleus,* MCZ 999; (2) *G. kingi,* MCZ 14834, 1452; (3) *G. liocephalus,* MCZ 24514a–c; (4) *G. multicarinatus,* MCZ 32250, 63657, and two unnumbered; (1) *G. imbricatus,* MCZ 97400; (1) *G. monticolus,* MCZ 15467; (1) *G. moreleti,* MCZ 49958.
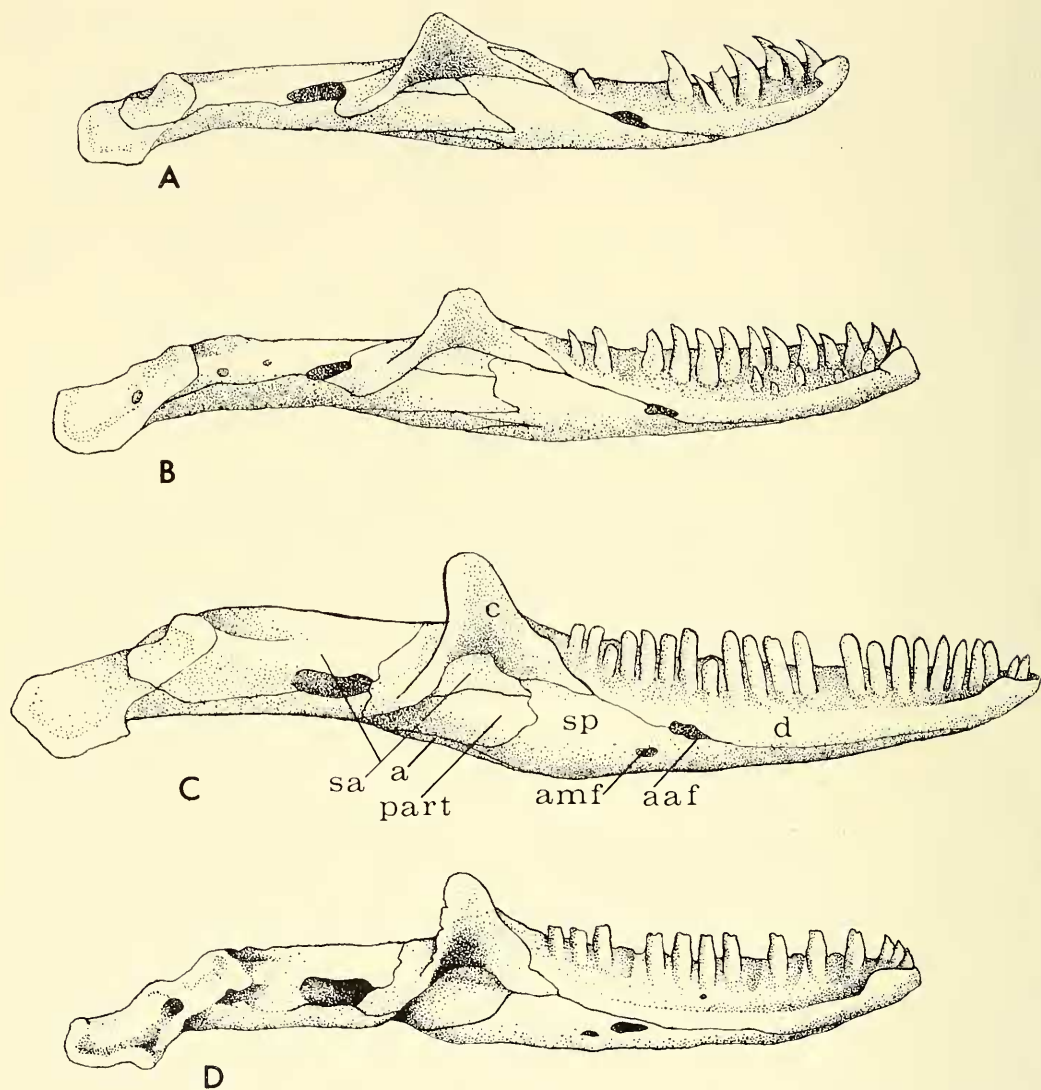
Figure 4. Mandibles of recent anguids in lingual view: A, *Anguis fragilis*, MCZ 37174; B, *Ophisaurus gracilis*, MCZ 15836; C, *Gerrhonotus (Barisia) imbricatus imbricatus*, MCZ 97400; D, *Diploglossus barbouri*, MCZ 7367a. Note that in formation of the anterior inferior alveolar mental foramen the dentary takes part in all except *Diploglossus*. All × 6. For abbreviations see p. 147.

Skull: Teeth in most species of *Gerrhonotus* recurved and somewhat pointed in anterior part of jaws, but becoming erect with chisel-shaped, laterally compressed crowns posteriad. *Abronia* has pointed, widely spaced teeth (but not to the extent observed in *Anguis* or in *Ophisaurus harti*). Pterygoids toothed in *G. (Gerrhonotus)* and rarely in *G. (Barisia)*; pterygoids robust with short palatine processes, closely approaching each other in *G. liocephalus* (Fig. 2a), widely separated in *Abronia*, and intermediate in *G. (Barisia)* and other *G. (Gerrhonotus)*. No premaxillary foramina;
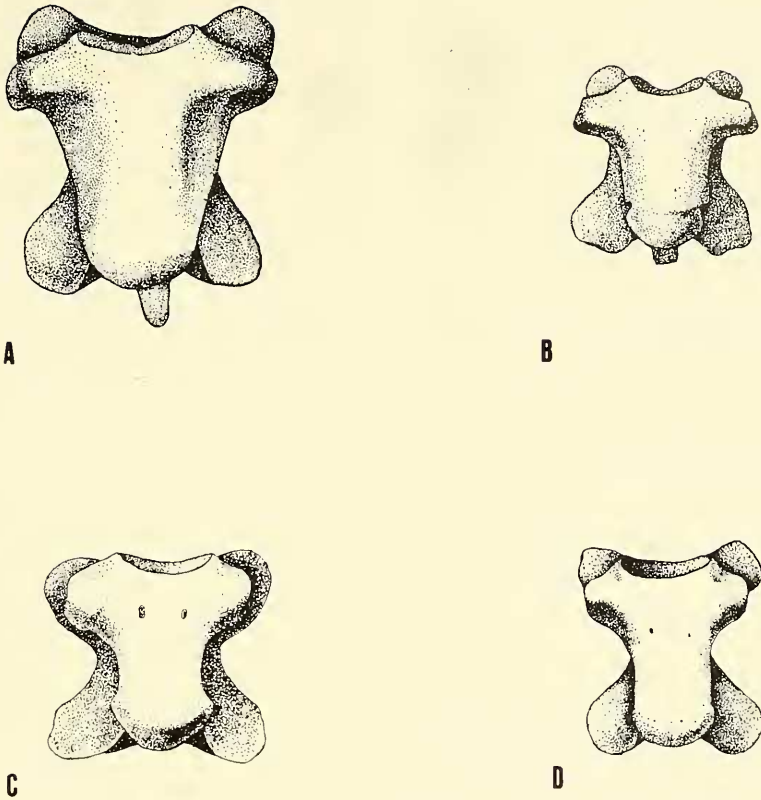
Figure 5. Trunk vertebrae of some onguids in ventral view: A, *Diploglossus monotropis*, MCZ 22912; B, *Gerrhonotus multicarinatus*, MCZ, unnumbered; C, *Ophisaurus ventralis*, MCZ 55509; D, *Anguis fragilis*, MCZ 37174. Note ventrally flattened centra in C and D, small exposure of condylar ball in A; not to scale.

frontals fused with concave orbital borders; olfactory process of frontal in contact with dorsal process of palatine bone. Maxilla and frontal in contact in *G. liocephalus* and also in the single specimen of *Abronia deppii* (Tihen, 1949, states that frontals are narrowly separated from maxilla in *Abronia*); parietal foramen present; postfrontal and postorbital separate, with postorbital gaining narrow exit into the orbit; jugal with well-developed posterior process. Surangular and articular usually fused, but the two bones may be separate or fused intraspecifically in *G. kingi*; surangular well or moderately in advance of labial dentary process of coronoid; labial dentary process of coronoid well developed

in all members of *Gerrhonotus* (Fig. 3c) and *Abronia*; anterior inferior alveolar foramen bordered above by dentary, below by splenial; anterior supra-angular foramen on labial surface not in contact with dentary (Fig. 4c).

Vertebrae: About 30 presacral vertebrae (Fig. 5b). Counts were possible on only the following species: *Abronia deppii* (27), *Gerrhonotus coeruleus* (26), *G. kingi* (30), *G. monticolus* (27), *G. moreleti* (26). Two sacrals with distal ends of transverse processes in contact; first caudals with chevrons located on pedicels; pedicels located on centrum right next to or confluent with condyle. Ribs without tubera costarum.

Epidermal scalation: No frontonasal and

frontal contact in most; in some species of subgenus *G.* (*Barisia*) no azygous fronto-nasal present at all. Frontonasal and frontal contact observed in: *Gerrhonotus liocephalus infernalis, G. monticolus, G. moreleti temporalis,* and *G. m. salvadorensis.* Left and right frontoparietals closely approaching each other or in narrow contact, as in *G. liocephalus loweryi, G. liocephalus infernalis, G. coeruleus,* and *Abronia deppii;* interparietal and occipital contact in all.

Body scales arranged in transverse bands, dorsals often with keels; lateral fold present in *Gerrhonotus,* but weakly developed or absent in *Abronia.*

Osteoscutes: Rectangular with gliding surface well developed in *Gerrhonotus,* but degenerate in *Abronia.* Gliding surface in shape of anterior transverse band. Lateral bevels prominent and indicative of overlap between adjacent osteoscutes. No lateral suturing present between osteoscutes.

Diploglossus, Wetmorena, and Ophiodes

Osteological material. (2) *Diploglossus monotropis,* MCZ 29682, 22912; (1) *D. badius,* MCZ 55722; (2) *D. barbouri,* MCZ 3767-a, 3767-c; (3) *D. costatus,* MCZ 63562, 65069, 65006; (3) *D. crusculus,* MCZ 7355, 45208, and one with no number; (1) *D. darlingtoni,* MCZ 57750; (1) *D. d. delasagra,* MCZ 38597; (3) *D. hewardi,* MCZ 7356, 7366, and one with no number; (7) *D. pleeii,* MCZ 36233, 36253 and five with no numbers; (1) *D. sepsoides,* MCZ 57056. (1) *Wetmorena haetiana,* MCZ 38270. (2) *Ophiodes striatus,* MCZ 20669, 7271.

Skull: Teeth ranging in these forms from robust crushing type with blunt crowns, as in *Diploglossus montiserrati* and *D. crusculus maculatus,* to teeth with pointed apices in *Ophiodes striatus;* in majority of forms teeth moderately robust with laterally compressed, chisel-shaped cutting edges; in all examined forms crowns with striations; no teeth on palate (Fig. 2d); pterygoids robust, closely approaching one another on midline; premaxillary foramina present;

frontals separate; dorsal process of palatine in contact with olfactory process of frontal; parietal foramen present; postorbitals and postfrontals in most forms distinct, but fused in *Ophiodes* and *Diploglossus pleeii,* with postfrontal entering into the orbit; jugal with well-developed posterior process, except in *Ophiodes* where it is ill-defined; surangular, prearticular, and articular usually fused (Fig. 3d), with unfused condition occurring sporadically; surangular in advance of anterior coronoid process; anterior labial process of coronoid not well developed and dorsal process well forward on this bone because of backward extension of the dentary; anterior inferior alveolar foramen of mandible bounded above and below by splenial (Fig. 4b). Anterior supra-angular foramen on the labial surface in contact with the dentary.

Vertebrae: Presacrals in thirties and forties in *Diploglossus,* but 72–74 in *Ophiodes striatus.* The following individual counts have been made: *Diploglossus barbouri* (34), *D. badius* (33), *D. costatus* (31), *D. crusculus* (33), *D. monotropis* (32), *D. d. delasagra* (43), *D. pleeii* (40), *D. sepsoides* (38). Two sacrals with distal end of transverse processes in close contact, even in the limbless *Ophiodes striatus.* Chevrons not fused to sacral vertebrae but joined to short, stubby pedicels. Ribs lacking tubera costarum in all species including *O. striatus.*

Centra of individual presacrals triangular in ventral view, not flattened but central portion slightly raised, slight constriction present between centrum and condyle (Fig. 5a). Caudals with unfused chevrons attached to pedicels, the latter somewhat removed from the condyle but closer to it than in *Ophisaurus* or *Anguis.*

Head scalation (Fig. 1): Frontonasal when present in contact with frontal; in *Ophiodes* as well as in all island forms frontonasal and two prefrontals fused (with a single exception noted by Underwood, 1959, p. 7). In holotype of *Diploglossus darlingtoni* these three scales
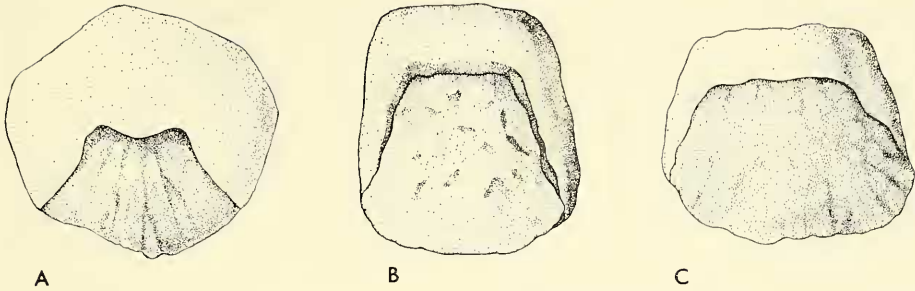
Figure 6. Middorsal body osteoscutes of recent onguids: A, *Diploglossus monotropis*, MCZ 29682, $\times$ 8; B, *Ophisaurus attenuatus attenuatus*, MCZ 5548b, $\times$ 17; C, *Anguis fragilis*, MCZ 3958, $\times$ 17. Note close resemblance between B and C, and unique medial convexity of gliding surface of A, occurring only in Diploglossinae.

separate, but fused in other specimens; frontoparietals widely separated, but not to the extent noted for *Ophisaurus* or *Anguis;* scales relatively much larger than in latter two genera; interparietal large, in contact with small occipital.

Body scales: In situ cycloid, skink-like in general appearance; lateral fold absent; keels present in a number of species, e.g., *D. monotropis, D. hewardi;* keels absent in *O. striatus.*

Body osteoscutes: With rounded outlines; anterior smooth gliding surface semicircular with posteromedial peak directed into sculptured surface that is especially prominent in dorsomedial scutes (Fig. 6a).

Discussion. Gerrhonotus and *Abronia* exhibit a number of cranial characters that are in strong contrast to conditions found in other Recent anguids. The unique premaxillary foramen of other Recent anguids is absent in these two genera (Fig. 2). In addition, fused frontals with prominent concave borders are found only in *Gerrhonotus* and *Abronia,* and here alone do the frontoparietal scales make a narrow contact (Fig. 12b). These two genera (especially *Gerrhonotus*) do, however, have body osteoscutes essentially the same as those in *Ophisaurus.* In both of these groups the osteoscutes are thick, bony, and rectangular, with a well-defined gliding surface in the shape of an anterior transverse band. These osteoscutes are beveled laterally where adjacent scutes overlapped, and no visible evidence of suturing between osteoscutes occurs. Both ophisaurs and *Gerrhonotus* have a lateral fold that connects the dorsal and ventral armor and apparently allows for greater mobility in these heavily armored forms. Where osteoscutes are not well developed, as in *Abronia,* the lateral fold is weak or absent.

Aside from body scutellation and the presence of teeth on the pterygoids, *Ophisaurus* shows no special resemblance to *Gerrhonotus.* However, the ophisaurs do have a great number of characters in common with *Anguis fragilis* that sets them apart from other anguids: (1) the postorbital is excluded from the orbit; (2) the olfactory process of the frontals fails to meet the dorsal process of the palatine; (3) the palatine process of the pterygoid is placed well anteriad of the maxillary process of the same bone, and the former process exceeds one-third the total length of the pterygoid; (4) the ribs have proximal posterior processes (tubera costarum) for muscle attachment; (5) only a single functional sacral vertebra, of similar shape, is present in both *Anguis* and *Ophisaurus;* (6) the caudal vertebrae have hemal arches fused to centra; (7) the frontoparietal scales are small and placed well laterad; (8) there is a close resemblance between the mandibles of the two genera in regard to proportion of dentary to post-dentary

portion and in regard to sutural contact between the above parts (Fig. 3a-b). Other characters not unique to the above forms, but shared with *Diploglossus* are: (1) paired frontals; (2) premaxillary foramen present. Also in *Anguis* as well as in *Ophisaurus*, but not in *Diploglossus*, and shared with some species of *Gerrhonotus*, the maxilla is not in contact with the frontal.

The main reason given by McDowell and Bogert (1954, p. 130, fig. 43) for placing *Anguis* in a subfamily of its own, the Anguinae, was the absence of a lateral fold and the superficially *Diploglossus*-like body scalation. However, this condition was regarded as degenerate by these authors, and they regarded the slow-worm as a specialized derivative of the ophisaurs. It is true that neither *Diploglossus* nor *Anguis* has a lateral fold, but the resemblance in osteoscutes is superficial. The isolated osteoscutes of *Diploglossus* are in strong contrast to those of *Anguis* and all other Recent anguids. Only in the diploglossines does the posterior margin of the much enlarged gliding surface have a posteriorly-directed peak (Fig. 6) where it meets the sculptured area of the osteoscutes. The osteoscutes of *Anguis* may be regarded as degenerate ophisaurine scutes in which the scutes are less rectangular, thinner, and have less prominent gliding surfaces. *Anguis* also exhibits a number of other degenerate features: lack of teeth on the palate, further reduced limb girdles, and absence of an external ear opening (also lacking in *O. koellikeri*). Further support of a close relationship between the ophisaurs and *Anguis* comes from Camp's studies on throat musculature (1923, p. 373), in which he states: "*Ophisaurus anguis* and *Anguis fragilis* are similar to each other and somewhat different from both *Ophiodes* and *Gerrhonotus*." He also notes (p. 340) that only in *Anguis* and *Ophisaurus* are all traces of the third branchial arches of the visceral skeleton lost. That the great number of characters common for both *Ophisaurus* and *Anguis*

is not the result of convergence due to limblessness is supported by the fact that the limbless diploglossine *Ophiodes* displays none of them. However, ventrally flattened vertebral centra and pointed recurved teeth appear to be specializations associated with limbless existence. Aside from *Abronia*, pointed teeth occur only in the limbless anguids, and all these forms have ventrally-flattened vertebral centra. The ophisaurs exhibit the greatest number of characters that may be regarded with some certainty as primitive for anguids as well as for all lizards, including paired frontals, teeth on palatines, pterygoids, and vomers. Vomerine teeth occur only in *Ophisaurus apodus*. Also, the ophisaurs appear to be somewhat intermediate between *Gerrhonotus* and the diploglossines. The ophisaurs share a similar body scutellation, the presence of a lateral fold, and a toothed pterygoid with the former group, and the presence of a premaxillary foramen and paired frontals with straight orbital borders with the latter.

The diploglossines differ from the ophisaurs and *Anguis* in the eight points in common listed above, and from *Abronia* and *Gerrhonotus* in having a premaxilliary foramen, paired frontals, and no lateral fold. They differ from all other anguids in having unique osteoscutes, with the posterior margin of the gliding surface having a posteriorly-directed peak, in having the anterior inferior alveolar foramen wholly on the splenial, and a tendency toward postorbital and postfrontal fusion. The diploglossines appear to be degenerate in the complete loss of palatal teeth in all members.

From this survey of Recent anguids, it appears that body scutellation is similar in the different groups of Recent anguids, and is evidence not always in accord with that from cranial and postcranial osteology. Scutellation in anguid classification should be utilized only in conjunction with evidence from osteology and soft anatomy.

Summary. (1) *Anguis* and *Ophisaurus*

are very closely related, in spite of different body scutellation in the two forms and the absence of a lateral fold in *Anguis.*

(2) *Ophisaurus* exhibits characters intermediate between the diploglossines and the Recent limbed gerrhonotines, sharing the separate frontals and the presence of a premaxillary foramen with the former and a similar body scutellation, lateral fold, and toothed palatal elements with the latter.

(3) The osteoscutes of the diploglossines are unique among Recent anguids. The osteoscutes of *Ophisaurus* and *Gerrhonotus* are similar, and those of *Anguis* represent a highly degenerate version of this type. Osteoscutes of all fossil anguids resemble those of *Ophisaurus* and *Gerrhonotus.*

(4) There is no justification for regarding the ophisaurs as closer related either to the limbed gerrhonotines or to the diploglossines, or to group these forms in the same subfamily with either of the above.

(5) On the basis of data presented above, the Recent forms are best divided into three subfamilies:

    a) The Gerrhonotinae (including the Recent limbed gerrhonotines of this paper, *Gerrhonotus, Abronia,* and tentatively *Coloptychon;* the type and only specimen of the latter, in the Humboldt Museum, Berlin, is lost).

    b) The Diploglossinae (including *Diploglossus, Ophiodes,* and *Wetmorena*).

    c) The Anguinae (including the genera *Ophisaurus and Anguis*).

It is now of interest to see whether or not the fossil forms can be placed in this classification, and what modifications they may suggest.

DESCRIBED NORTH AMERICAN FOSSIL GENERA AND SPECIES

Gervais (1859) was the first to describe a fossil referable to the Anguidae. He gave the name *Placosaurus rugosus* to a speci-

men (from the Upper Eocene of Sainte Aldegarde, France) consisting of skull fragments and osteoscutes. Similar fossils from Europe were described under the names of *Diploglossus cadurcensis* de Stefano (1904), *Plestiodon cadurcensis, Necrodasypus galliae* Filhol (1877, 1894), and *Varanus margariticeps* Gervais (1876). Boulenger (1918) regarded all of these fossils as placosaurs.

The first to describe fossil anguids from North America was Marsh (1871). He referred Middle Eocene fossil remains from the Bridger Formation of Wyoming to a new genus with four species: *Glyptosaurus sylvestris, G. ocellatus, G. nodosus,* and *G. anceps.* Marsh (1872, p. 6) added a further new species, *G. princeps,* and in the same paper described *Oreosaurus vagans* (the preoccupied generic name *Oreosaurus* was later changed to *Xestops* by Cope, 1873). In Part II of the same paper Marsh added three more species to *Glyptosaurus* and four more to *Xestops* (=*Oreosaurus*). Gilmore (1928, p. 94) synonymized *G. ocellatus* with *G. sylvestris* and referred *G. anceps* to the Amphisbaenidae. With the exception of *X. vagans,* the specimens referred to *Xestops* by Marsh consist of very fragmentary lower jaws, vertebrae, and osteoscutes. Marsh made no reference as to where among the Recent families the affinity of the fossils lay, but considered *Glyptosaurus* and *Xestops* as related forms.

Cope (1873, p. 5) described a new genus and species, *Peltosaurus granulosus,* from the Oligocene Cedar Creek beds of Colorado, and later (1884, p. 772) referred the fossils to his family Gerrhonotidae (see above).

Gilmore (1928) was the first to study all available North American fossil lizard material and to examine the interrelationships among the fossil forms and their affinities to Recent groups. Gilmore recognized four fossil genera in the family Anguidae and the following species under these genera:

Glyptosaurus sylvestris Marsh 1871

G.   *nodosus* Marsh 1871
G.   *princeps* Marsh 1872
G.   *rugosus* Marsh 1872
G.   *sphenodon* Marsh 1872
G.   *tuberculatus* Douglass 1903
G.   *obtusidens* Loomis 1907
G.   *montanus* Douglass 1908
G.   *hillsi* Gilmore 1928
G.   *giganteus* Gilmore 1928
Peltosaurus granulosus Cope 1873
P.   *abbottii* Gilmore 1928
P.   (?) *piger* Gilmore 1928
Xestops vagans Marsh 1872
X.   (?) *gracilis* Marsh 1872
X.   (?) *lentus* Marsh 1872
X.   (?) *microdus* Marsh 1872
X.   (?) *minutus* Marsh 1872
X.   (?) *pawneensis* Gilmore 1928
Melanosaurus maximus Gilmore 1928

Only a few new taxa have been added to Gilmore's list of fossil anguids. Hecht (1959, pp. 132–134) described *Dimetopisaurus wyomingensis* from the Middle Eocene Bridger Formation sediments at Tabernacle Butte in Wyoming and regarded this species as related to Recent *Ophisaurus*. Estes (1963b, pp. 676–680) described *Paragerrhonotus ricardensis* from the Lower Pliocene Barstow Formation of California and suggested a possible resemblance to the xenosaurs. *Glyptosaurus donohoei* was described by White (1952, pp. 186–189) from the Lower Eocene deposits of the Boysen Reservoir area, Shoshone, Wyoming. *Peltosaurus jepseni* (Gilmore, 1942) was described from the Upper Paleocene Silver Coulee beds of the Polecat Bench Formation, Park County, Wyoming. Gilmore (1938) also described a new species, *Xestops piercei*, from the Lower Eocene Wasatch Formation of Wyoming. *Melanosaurus* has had no additional species described, but Hecht (1959) recognized this genus on the basis of scutes, as well as *Xestops* and *Peltosaurus*, from the Middle Eocene Bridger Formation at Tabernacle Butte. *Peltosaurus floridanus* (Vanzolini, 1952, p. 457) is probably a misplaced *P.*

granulosus from the White River Formation, since it is unlike the other Thomas Farm Miocene specimens in preservation, and is indistinguishable from *P. granulosus*, as Estes has noted (1963a, pp. 252–253).

Although the list of new genera and species of North American fossil anguids has not increased appreciably, a number of fossil fragments has been referred to extant genera or species, especially to the genus *Ophisaurus*.

Auffenberg (1955, pp. 133–136) refers fossil vertebrae from the Pleistocene of Florida to two Recent species of *Ophisaurus*, *O. ventralis* and *O. compressus*. His identification rests on neural spine angles formed with the centrum and on ratios of centrum length to width. Holman (1958, p. 278) lists *Ophisaurus ventralis* on his faunal list from the Pleistocene Saber-tooth Cave of Florida. His *Ophisaurus* material consists of two dentaries and three thoracic vertebrae, and his identification rests on measurements of vertebrae adopted from Auffenberg. Etheridge (1960, pp. 46–67; 1961, pp. 179–186) refers vertebrae from the Upper Pliocene and Pleistocene of Kansas and the Pleistocene of Oklahoma to *Ophisaurus attenuatus*, again utilizing Auffenberg's method of identification.

Dentaries from the Upper Cretaceous Lance Formation of eastern Wyoming are compared with Recent *Gerrhonotus* by Estes (1964, pp. 122–125). His main criterion for distinguishing this form from *"Peltosaurus" piger*, a more abundant form in the Lance, is tooth structure. McKenna (1960, p. 10) also lists *Gerrhonotus* and *Peltosaurus* in his faunal list of the Lower Eocene of Northwestern Colorado, from identifications provided by Estes. Gazin (1956, p. 12) refers four dentary fragments, two maxillary fragments, and a premaxilla to the family Anguidae from the Upper Paleocene Bison Basin locality of Wyoming. This deposit is of Tiffanian (late Paleocene) age.

Pancelosaurus new genus

*Type species of the genus. Peltosaurus?
piger* Gilmore 1928

Geological range. Late Cretaceous—Middle Oligocene.

Referred species. Pancelosaurus piger
(Upper Cretaceous-Paleocene), *P. pawneensis* (Oligocene).

Etymology. Hungarian, *pancél*—armor;
Greek, *sauros*—lizard.

Pancelosaurus piger (Gilmore) 1928

Peltosaurus? piger Gilmore 1928
Odaxosaurus obliquus Gilmore 1928
Peltosaurus jepseni Gilmore 1942
Peltosaurus piger Estes 1964

Holotype. USNM 10687. The specimen
consists of the posterior portion of the
right dentary, containing six teeth and
spaces for three others.

Type locality. "Peterson's quarry," Lance
Creek, Niobrara County, Wyoming.

Horizon. Lance Formation, Upper Cretaceous.

Introduction. Gilmore (1928, p. 316)
described a new species, *Peltosaurus? piger*,
on the basis of two jaw fragments, a right
dentary, USNM 10687, and a right maxilla,
USNM 10688, both from the Upper Cretaceous Lance Formation of Wyoming.
The tentative generic assignment of this
new species rested on tooth structure,
which according to Gilmore was "remarkably like that of *Peltosaurus granulosus*."

Estes (1964, pp. 119–122) described the
parietal and osteoscutes of this lizard, and
gave a more detailed description of the
maxilla and dentary based on a large number of specimens from the Lance Formation.

Identification of Skeletal Elements

The fossils at the localities from which
Pancelosaurus piger is known consist of
dissociated, often fragmentary individual
bones. Practically no two individual
skeletal elements articulate with one another; therefore assignment of individual
skeletal elements to this genus and species

rests on comparative study. The holotype
of *P. piger* is a dentary that bears teeth;
therefore, the assignment of marginal tooth-bearing bones such as maxillae and premaxillae to the above species is relatively
easy on the basis of tooth comparison.
Body osteoscutes and skull elements fused
with the covering osteoscutes (parietals
and frontals) are easily identified as
anguid. From the Lance Formation only
two anguid lizards are known (Estes,
1964): *Pancelosaurus piger* and a form in
which the structure of the teeth and dentaries compares well with *Gerrhonotus*. The
former is by far the more abundant of the
two. The Lance frontals are not similar to
those of the Recent *Gerrhonotus*, and also
their size is more consistent with reference
to *P. piger*. No other type of anguid frontal is known from the Lance Formation.
The situation in the Hell Creek Formation
(Bug Creek Anthills local fauna) is essentially the same as in the Lance (Estes,
Berberian, and Meszoely, 1969; Sloan and
Van Valen, 1965).

An MCZ collection of lower vertebrate
remains from the early Paleocene Bison
Basin locality (Gazin, 1956) consists
mostly of skeletal elements referable to
Pancelosaurus piger; other lizard remains
are extremely rare. This greatly facilitates
the assignment of individual bones that do
not occur in the Lance or the Bug Creek
Anthills to *P. piger,* especially if these
elements occur at the same frequency as
those elements that can be assigned with
certainty to this species.

Bones that are not associated with osteoscutes and do not bear marginal teeth have
been assigned to *P. piger* by careful comparison with disarticulated Recent skeletal
material and with the same elements of
articulated Eocene and Oligocene anguids.

Description and Comparison
of Skeletal Elements

Since no significant differences occur
among bones of *Pancelosaurus piger* from
Lance Formation, Hell Creek Formation,

or Bison Basin localities, a general description is given below.

Dentary (Fig. 10c): Estes (1964, p. 120) describes the dentary as follows: "The dentary is robust; the Meckelian fossa is ventral anteriorly and was evidently covered by the splenial over almost its entire length. The intramandibular septum has a free ventral border, the posterior border of which is notched for the Meckelian cartilage. The anterior inferior alveolar foramen forms a notch on the dental ridge below the sixth or seventh tooth from the rear. The external face of the dentary has a large dorsal notch for the coronoid, extending anteriorly to the level of the second tooth from the rear. The teeth are pleurodont, closely spaced, anteroposteriorly compressed; the maximum number of dentary teeth is nineteen. The shafts of the teeth exclusive of the crown are lingually expanded and bulbous. The crown is relatively small and has an enameloid covering. The most anterior teeth are slightly procumbent and are less lingually expanded than the posterior ones. The tooth bases are subrectangular and the shafts are relatively thick. The tooth apices have horizontal cutting edges that are set at a slight angle to each other, trending anteromedially-posterolaterally, and the crowns are wrinkled lingually and labially."

Comparison. The teeth of *Pancelosaurus piger* resemble most closely those of the fossil *Peltosaurus granulosus.* However, the latter lacks the enameloid dark brown covering of the former. Dark colored enameloid material is also present on the apices of the teeth of *Diploglossus monotropis,* and seems to be independent of tooth preservation. In having a free ventral border to the intramandibular septum, *P. piger* is in agreement with the Recent forms *Diploglossus* and *Gerrhonotus,* but is in strong contrast to *P. granulosus,* in which the ventral border of the septum is mostly fused to the dentary; also, in the latter form the Meckelian fossa is more widely open on the lingual side than in *P.*

piger. The anterior extremity of the notch on this septum extends to the third tooth from the back in *P. piger* and to the fifth from the back in *P. granulosus.* The posterior margin of the dentary also presents a different outline from that of *P. granulosus,* indicating that the contact of the dentary with the post-dentary bones was different in the two fossil forms. In this last respect, *P. piger* shows a particular resemblance to *Gerrhonotus* and *Ophisaurus* in the far anterior extent of the angular-surangular notch (cf. Figs. 3b-c, 10c, 17).

Maxilla (Figs. 7b, 9c, 10a-b): Estes (1964, pp. 120–121) describes the maxilla as follows: "The maxilla is robust, and bears thirteen to fifteen teeth like those of the dentary. Externally it is faintly wrinkled by osteodermal scars. The nasal process is relatively low. It rises abruptly behind the naris, rounds off dorsally, and slopes rapidly downward to the posterior tip. There is a slight supradental shelf and a strong palatine process. In dorsal view the posterior half of the bone is strongly expanded, twisted laterally, and bears a deep groove for the jugal. The premaxillary process is bifid, with an external portion fitting into the premaxilla, and a medial vomerine portion."

Comparison. In having a relatively short premaxillary process with a prominent bifid anterior extremity, the maxilla of *Pancelosaurus piger* resembles that of the Recent *Diploglossus* and *Ophisaurus.* This same process is elongate and barely bifurcate in *Gerrhonotus.* Since a premaxillary foramen is present between maxilla and premaxilla in both of the former Recent genera, the above features are indicative of the presence of this foramen in *P. piger.* The oblique ridge dividing the dorsal surface of the supradental shelf into anterior and posterior portions is well developed in all anguids excepting *Gerrhonotus,* in which it has a feeble development. Also, in this latter form the tooth-bearing portion of the maxilla posterior to the facial process
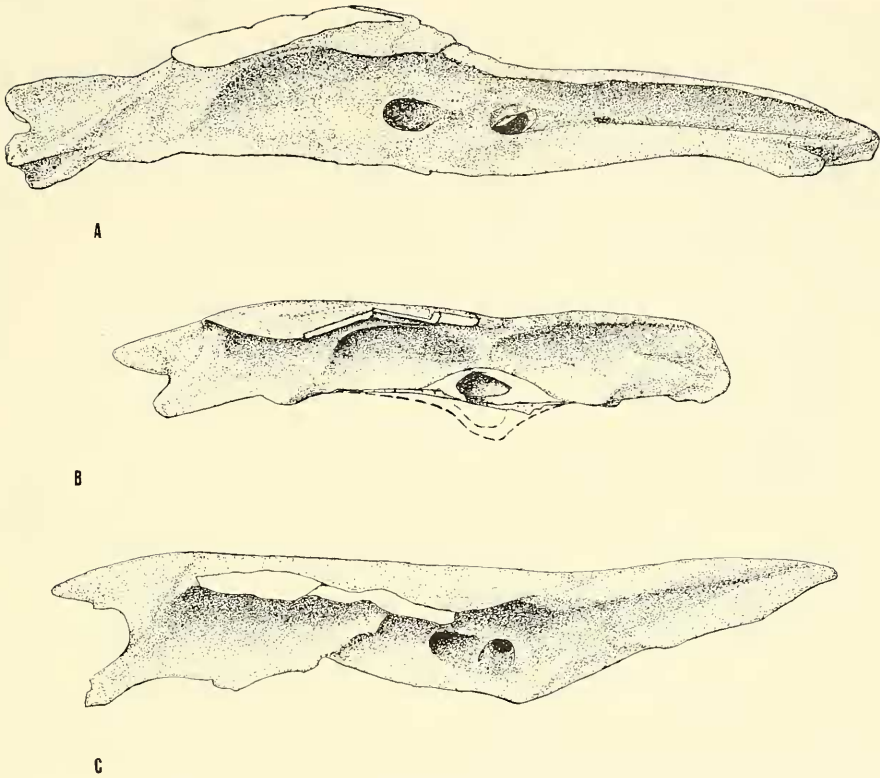
Figure 7. Maxillae, in dorsal view, of recent and fossil anguids. A, *Gerrhanatus liacephalus*, Recent, MCZ 24518; B, *Pancelasaurus piger*, n. gen., UC 49772; C, *Diploglossus hewardii*, Recent, MCZ 7356. Note resemblance between B and C, and the bifid anterior end of B, indicating the possible existence of a premaxillary foramen. Ascending processes of maxillae broken in all to allow view of internal structures. All × 8.

is relatively very long, whereas this same area is very short in *P. piger*. In *Ophisaurus* it has approximately the same proportion as in *P. piger*, while in *Diploglossus* its relative length is in between those of the above forms. The tooth count of 13–15 in *P. piger* is very low for anguids, equalled only by some species of *Diploglossus*. This tooth count is exceeded in all other Recent anguids except *Anguis* and in fossils where a tooth count is available. *Peltosaurus granulosus* and *Melanosaurus maximus* have a maxillary tooth count of 16–17. The low tooth count and the short maxillary ramus posterior to the facial process apparently indicate that *P. piger* was a short-nosed, broad-faced anguid lizard.

Frontal (Figs. 8c, 12a): Frontals distinct with almost straight orbital borders somewhat expanded posteriorly. Osteoscutes fused to underlying bone and sculptured with irregular pits and ridges. Imprint of large frontoparietal scale extending anteriorly less than one-third the total length of frontal. Frontoparietal separated from metopic suture by much smaller mesial interparietal impression. At anterior extremity of frontal, V-shaped incision marks point of overlap by nasal bone. Lateral to V-shaped incision, frontal devoid of osteoscutal crust, indicating position of prefrontal osteoscute. Very small portions of posterolateral corner of frontal also devoid of sculpture.
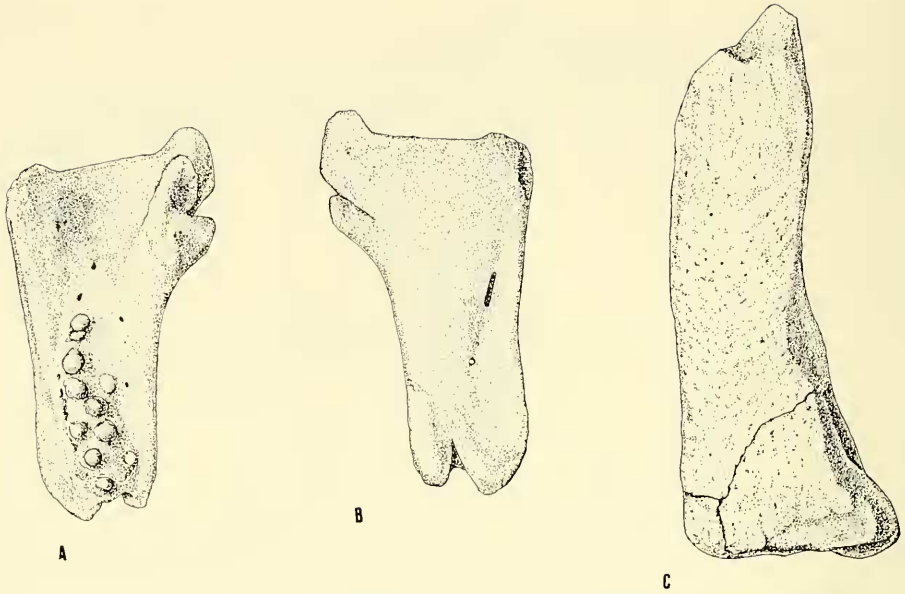
Figure 8. *Pancelosaurus piger,* n. gen. A, left palatine, ventral view, MCZ 3495; B, the same, dorsal view; C, right frontal, dorsal view, UC 61414; A–B, Upper Paleocene Bison Basin deposits, Wyoming; C, Upper Cretaceous Lance Formation, Wyoming. All × 8.

In lateral view frontal displays two deep incisions. Large anterior prefrontal incision occupies over half and smaller prefrontal incision one-third total length of orbital border of frontal bone. The above incisions separated by about one-seventh total length of this bone. Olfactory processes on ventral surface well developed, but separated ventrally.

Comparison. The frontals of *Pancelosaurus piger* resemble closely those of Recent *Diploglossus;* they agree in general outline, in epidermal scalation as indicated by impressions on the osteoscutal surface, in being suturally distinct, and in having nearly identical sculpture on the osteoscutes covering these bones.

In *Pancelosaurus piger,* as well as in *Diploglossus,* the frontoparietal scale impressions are large, and left and right scales are well separated from one another at the midline by the interparietal scale impression. Similar scalation is also found in the fossil *Xestops vagans* and the Recent ophisaurs, *Anguis,* and diploglossines. The

sculpture of the osteoscutal surface in *P. piger* is of irregular pits and ridges, in strong contrast to the raised tubercular mounds on the frontals of *X. vagans.*

In *Ophisaurus,* the frontoparietal epidermal impressions are much smaller and more widely separated than in *Pancelosaurus piger;* there is less correspondence in general outline, as well. The entire lateral edges of the *Ophisaurus* frontals are devoid of osteoscutes as a result of the presence of small, loosely-attached osteoscutes covering this area.

Pancelosaurus frontals share only a similar type of dermal sculpture with the fused, emarginate frontals of Recent *Gerrhonotus,* but in some members of *G.* (*Barisia*) the sculptured surface becomes much more pronounced than in any of the other Recent anguids or in *Pancelosaurus.*

The frontals of *Pancelosaurus piger* bear little resemblance to the large Eocene and Oligocene forms *Peltosaurus, Melanosaurus, Arpadosaurus* (n. gen., see p. 136), and *Glyptosaurus.* In *Glyptosaurus* the

osteoscutal crust is broken up into numerous polygonal plates, and in *Arpadosaurus* grooves on the osteoscutal crust indicate an epidermal scalation highly unusual among anguids. In *Melanosaurus* the epidermal scalation is not clear because of weak scale impression on dorsal surfaces of the frontal bone in all fossil specimens referable to this genus. However, the frontal bones are coossified in *Melanosaurus* and also differ in shape from those of *P. piger*. *Peltosaurus* also has coossified frontal bones and exhibits an epidermal scalation in which the two frontoparietal scales are in broad contact on the midline along almost their entire length.

Parietal (Figs. 9e, 16e): Parietal unpaired, with straight frontoparietal suture and gently concave lateral borders. Parietal table longer than wide, with over one-half of dorsal surface covered by osteoscutal crust. Supratemporal processes expanded, slightly exceeding frontoparietal suture in breadth. Faint grooves on osteoscutal crust indicate outline of interparietal, occipital, and parietal epidermal scales. Interparietal scale area a large, posteriorly-directed triangle, containing parietal foramen near apex. Occipital in contact with apex of interparietal, also triangular, but much smaller. Rest of osteoscutal crust occupied by two lateral parietal scale areas. On ventral surface anterior ridges converge posteromedially to form triangle; parietal fossa located at apex of triangle. Parietal fossa an anteriorly-directed oblique pit, located two-thirds of the way back on parietal table. Two small parallel ridges lead from posterior parietal notch to parietal fossa, forming shallow trough. Two posterior ridges follow lateroposterior border of parietal closely and merge with anterior ridges at point somewhat more than one-half the distance from anterior margin.

Comparison. The parietal of *Pancelosaurus piger*, like the frontals, bears the closest resemblance to that of the Recent *Diploglossus*. The sculpture of the osteoscutes fused with the bone resembles that found in the Recent forms and is in strong contrast to the tubercular mounds of *Xestops*, *Peltosaurus*, *Melanosaurus*, *Arpadosaurus*, and *Glyptosaurus*. The epidermal scale impressions on the osteoscutal surface also resemble those of the Recent forms. The interparietal impression is wide and large, whereas that of the occipital is very small. In *Peltosaurus granulosus* and in *Melanosaurus maximus* these two impressions are nearly the same size, and the interparietal impression is much narrower than in the Recent forms and *Pancelosaurus piger*. The osteoscutal crust covers over half of the parietal table in *P. piger*, as it does in *Diploglossus* and *Ophisaurus*; in *Gerrhonotus* less than half of the parietal table is covered by osteoscutes. In *Gerrhonotus*, this area is also much more elongated, and the supratemporal processes are less divergent than in *P. piger*. On the ventral surface a trough leads to the parietal fossa between two parallel ridges, which are the posterior extensions of the anterior ridges. This trough has the same relative length in *Diploglossus* and *P. piger*. The same trough is much shorter in *Ophisaurus* because of the very posterior location of the parietal fossa. In *G. liocephalus* there is no trough because the two anterior ridges join to form a single posterior median ridge. In *Peltosaurus granulosus* the situation is similar to that in *Pancelosaurus* and *Diploglossus*, but the proportions are different as a result of widening of the parietal table in the former.

Palatine (Fig. 8a, b): Palatine a spatulate bone with expanded anterior end; anterior margin of bone nearly straight. Ventral surface of bone bears a patch of tubercular teeth; tooth patch is two teeth wide and extends from posterior extremity to a little more than one-half entire length of bone. Point where the teeth end marks the beginning of broad depression that forms internal choana. On both sides of choanal depression edges of palatines
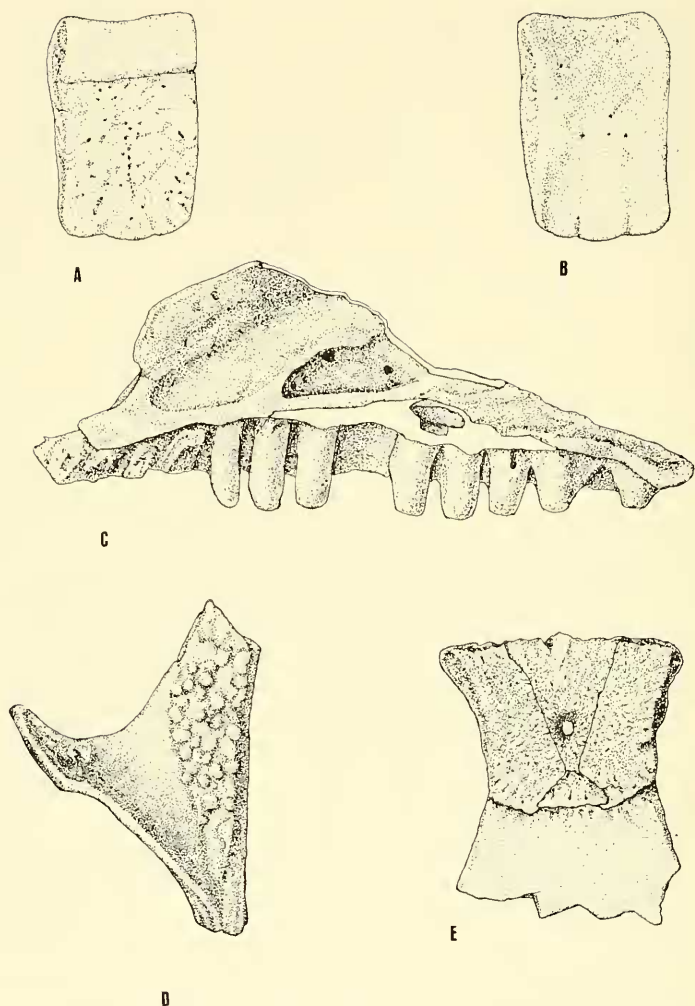
Figure 9. *Pancelasaurus piger*, n. gen. A, body osteoscute, dorsal view; UC 61414; B, the same, ventral view; C, maxilla in lingual view, UC 49772; D, right pterygoid, ventral view, MCZ 3497; E, parietal in dorsal view, MCZ 3498. A–B, Upper Cretaceous Hell Creek Formation, Montana; C, Upper Cretaceous Lance Formation, Wyoming; D, Upper Paleocene Bison Basin deposits, Wyoming. A–D × 8, E × 4.

curled ventrad; mesial edge bears small vomerine process, lateral edge with larger maxillary process. Latter process exhibits oval articular surface, which in Recent anguids is overlapped ventrally by maxilla. Oval articular surface bears anterior notch for the exit of superior alveolar nerve, which in Recent anguids enters maxilla at this point. Infraorbital canal completely surrounded by palatine bone as in all anguids; however, in majority of fossils this process damaged, giving appearance of notch to infraorbital foramen.

Comparison. In having a toothed palatine bone, *Pancelosaurus piger* agrees among the Recent forms only with *Ophisaurus*, in all species of which this bone bears teeth. Among the fossil forms toothed palatines appear to be the rule. *Arpadosaurus, Melanosaurus,* and *Peltosaurus* all
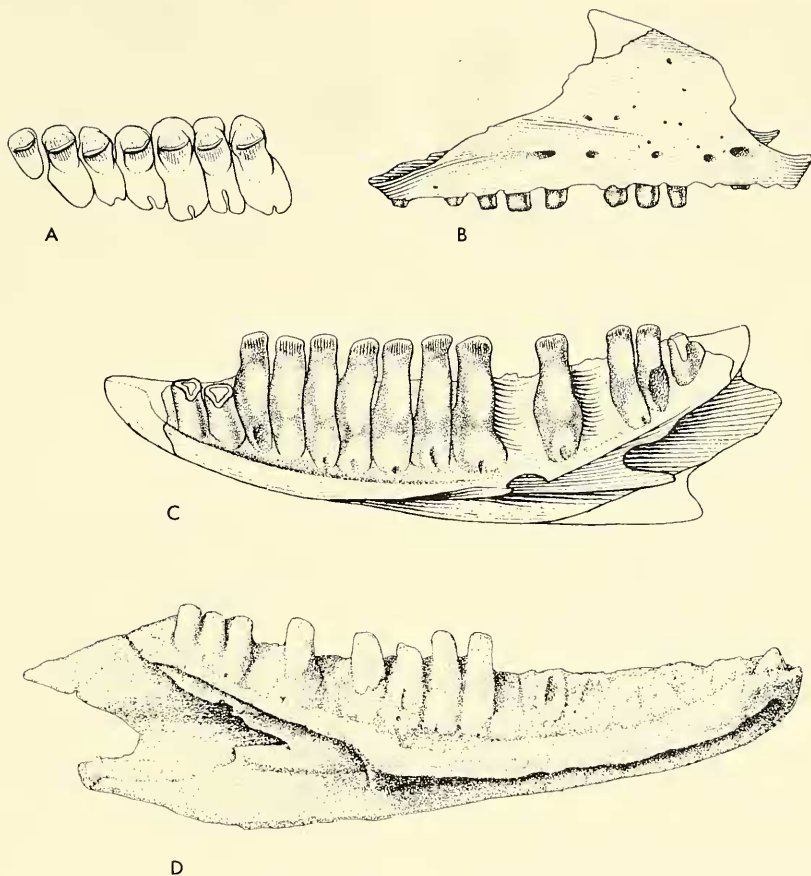
Figure 10. *Pancelosaurus piger*, n. gen. A, UC 47756, occlusal outline of seven posterior left dentary teeth; B, UC 49772, right maxilla, labial view; C, UC 47756, right dentary, lingual view; D, *Peltosaurus granulosus*, KU 1282, lingual view, left dentary. A–C from Estes, 1964, Upper Cretaceous Lance Formation, Wyoming; D, Oligocene, White River Formation, Colorado. All × 6.

bear teeth on the palatine; in other fossil genera the palatine bone is not known.

The general outline of palatine bones is similar in anguids, but in *Diploglossus* the choanal depressions extend posteriad more than half the entire length of this bone, while in the other Recent forms, as well as in *Pancelosaurus piger*, the choanal depression comprises less than one-half the total length of the palatine bone.

The infraorbital canal, in common with that of most anguimorphs, is a foramen rather than a notch on the maxillary process of the palatine. Anguids also usually have a relatively straight anterior margin to this bone, whereas in non-anguids the anterior margin of this same bone is often strongly slanted. A foramen on the maxillary process of the palatine was observed in all Recent forms, and in the fossil *Pancelosaurus piger*, *Peltosaurus granulosus*, and *Arpadosaurus* (in the other fossils this area is not observable).

Pterygoid (Fig. 9d): Pterygoids with patch of tubercular teeth along ventromedial margin. Tooth patch four to five teeth wide and extending to anterior extremity of pterygoid, thus forming con-

tinuous palatal tooth patches with palatines. Tooth-bearing area triangular, with lateral apex bearing anteriorly-directed ectopterygoid process. Dorsal surface of bone smooth with deep, triangular, anterolateral ectopterygoid incision.

Comparison. In having teeth, the pterygoids of *Pancelosaurus piger* resemble those of the Recent ophisaurs and members of the subgenus *Gerrhonotus*. Pterygoid teeth as well as palatine teeth are present in every fossil anguid in which this bone is known: *Glyptosaurus, Peltosaurus, Xestops* and *Melanosaurus*.

In *Pancelosaurus, Ophisaurus,* and *Anguis* the palatine process of the pterygoid extends well in front of the maxillary process; in other anguids the anterior extremities of the above processes are nearly in line.

Premaxilla (Fig. 11): Premaxilla an unpaired, anchor-shaped bone in anterior view, with broad nasal spine. Nasal spine constricted at its base. Rostral body relatively wide, with its anterior margin gently arched in dorsal view, lateral maxillary processes well developed. Maxillary processes bearing deep dorsal triangular incision for maxillae. Near base of nasal spine three posterolateral foramina present on each side.

Prominent medial suture present on lingual surface of nasal spine extending to posterior extremity of palatine process. Incisive process broken in all examined specimens. Premaxillary tooth count nine. Teeth essentially as described for other jaw elements. Large unpaired foramen present posterior to medial tooth, becoming paired at short distance from its origin.

Comparison. The rostral body of the premaxilla of *Pancelosaurus piger* is similar to that of the Recent *Diploglossus*. In both, the maxillary processes are elongated in dorsal view, and the outline of the anterior margin of the rostral body is gently arched. In Recent *Gerrhonotus* the rostral body is much shorter as a result of the shorter maxillary processes; hence there is

less participation by this bone in the formation of the external nares. In *Ophisaurus* the anterior border of the rostral body is not arched; the left and right sides meet at a strong angle to one another and present an inverted V in dorsal view. In *P. piger,* as in *Ophisaurus* and *Diploglossus,* there is a notch or constriction at the base of the nasal spine; in *Gerrhonotus* the base of the nasal spine is not constricted, but the spine emerges from the rostral body gradually, narrowing in a dorsoposterior direction. The rostral body is short and presents the same foreshortened triangular shape in *Melanosaurus* and *Peltosaurus* as in *Gerrhonotus*.

The palatine processes are not preserved in any *Pancelosaurus* specimens, and hence it cannot be determined with certainty if premaxillary foramina were present as in Recent *Ophisaurus, Diploglossus,* and *Anguis*. As indicated above, however, it is very possible that they were present.

Osteoscutes (Fig. 9a, b): Lateral body osteoscutes rectangular and sculptured with irregular pits and ridges. Smooth gliding surface occupies from one-fourth to almost one-half entire length of osteoscute. Prominent smooth oblique surfaces along lateral edges, one ventrally and the other dorsally located, indicate high degree of lateral overlap between adjacent osteoscutes. No evidence of lateral suturing. No keel present on any of the several hundred scutes so far discovered.

Middorsal body osteoscutes fan-shaped, unkeeled, and somewhat expanded posteriad. Extent of area occupied by the gliding surface is variable as above. Along both dorsolateral edges middorsal scutes bear smooth oblique surfaces indicating overlap on both sides by adjacent scutes.

Comparison. Osteoscutes of *Pancelosaurus piger* bear the closest resemblance to those of Recent *Gerrhonotus* and *Ophisaurus,* agreeing with the latter genera in the following characteristics:

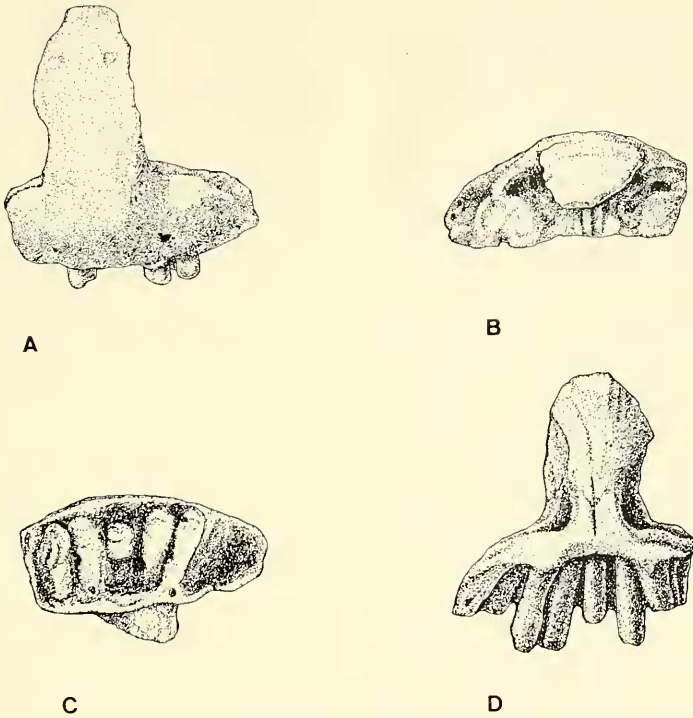(1) Sculpture consisting of pits and ridges.

Figure 11. *Poncelosaurus piger*, n. gen. MCZ 3690, premaxilla, A, anterior, B, dorsal, C, ventral, and D, posterior views. Bison Basin deposits, late Paleocene, Wyoming; × 8.

(2) Gliding surface in the shape of an anterior transverse band.

(3) Osteoscutes with rectangular outline.

(4) Prominent beveled lateral margins.

(5) No evidence of lateral suturing of osteoscutes to one another.

In all of these characters except number 1, osteoscutes of *Peltosaurus granulosus* agree with those of *P. piger*, but the former have a strikingly different sculpture, consisting of raised tubercular mounds.

Xestops vagans has sculpture of the osteoscutes identical to that of *Peltosaurus granulosus* and also agrees in most of the above points with *Pancelosaurus piger*, but in *X. vagans* the jagged edges of the osteoscutes are indicative of some lateral suturing; nevertheless they are beveled as well.

In *X. vagans* the osteoscutes are also more robust than in *P. piger* and are keeled.

Osteoscutes of the large Eocene and Oligocene fossils *Melanosaurus, Arpadosaurus,* and *Glyptosaurus* are also rectangular, and the gliding surface is arranged in the shape of a transverse band. Sculpture of the osteoscutes is the same in these forms as in *Xestops* and *Peltosaurus,* but in the former genera the tubercular mounds are often arranged in concentric rectangles. In *Glyptosaurus, Melanosaurus,* and *Arpadosaurus* a number of the osteoscutes bear keels. There is little lateral overlap in these forms between osteoscutes, and the lateral margins bear jagged edges indicative of lateral suturing.

The general appearance of the osteoscutes of *Pancelosaurus piger* is least similar to that of the Recent *Diploglossus.* In *Diploglossus* the osteoscutes are round

or ovoid and have a gliding surface with a concave posterior border with a prominent posterior peak. Sculpture of the osteoscutes is similar in *P. piger* and in *Diploglossus*.

Vertebrae: Thoracic vertebrae procoelous, robust, relatively short, and triangular in ventral view. Anterolateral corners of triangle strongly expanded laterally and bearing articular surfaces for ribs; rib articular surfaces dorsoventrally elongated. Ventrally, on both sides of subcentral keel, centrum bears lateral depressions; depressions extending along ventrolateral margin of centrum from rib bearers to condylar ball; condylar ball wide but with little ventral exposure. Neural arches moderately low, with zygapophyses ranging from nearly circular to subcircular; feebly-developed zygosphenes and zygantra present; prezygapophyses tilted at sharp angle upward and inward. Neural canal relatively large, exceeding height of centrum in anterior view, and breadth equal to cotylar depression; cotyle deeply excavated. Relative length of individual centra highly variable in available fossil sample, presumably corresponding to regional variations observable in Recent anguids.

Comparison. Trunk vertebrae of *Pancelosaurus piger* are not flattened ventrally as in the limbless *Ophisaurus*, *Anguis*, or *Ophiodes;* the midventral area of the centrum is convex as in the limbed forms *Gerrhonotus*, *Abronia*, and *Diploglossus*. *Pancelosaurus* was thus probably a limbed form. The vertebrae of *P. piger* are unique among anguids in having zygosphenes and zygantra. In having a wide condyle with little ventral exposure the vertebrae of *P. piger* resemble those of *Diploglossus*. Further comparisons are difficult to make as a result of similarity between trunk vertebrae of Recent limbed forms. There is also a high degree of regional variation in these forms along the vertebral column, which affects the shape of the individual vertebrae. In general, trunk vertebrae from the anterior part of the vertebral column are shorter and more triangular in outline.

Vertebrae of the large fossil forms such as *Melanosaurus* and *Glyptosaurus* are also triangular in ventral outline, but here the centrum is relatively shorter and more expanded anterolaterally than in *Pancelosaurus piger*. The condyle is also large in *Melanosaurus* and *Glyptosaurus* and dorsoventrally flattened, exceeding in breadth the centrum at the point where these two structures come in contact.

Discussion. Gilmore (1928, p. 126) provisionally referred a dentary and a maxilla from the Upper Cretaceous Lance Formation to the genus *Peltosaurus*, calling the new species *P.? piger*. McDowell and Bogert (1954, p. 133) not only questioned the generic assignment of this lizard, but considered it probably not anguid. Estes (1964, pp. 119–122) reinstated it in the Anguidae and referred it with more certainty to the genus *Peltosaurus*. However, at that time a number of the diagnostic cranial elements of this lizard were not known. Now that most of the skull bones are known, it appears certain that this form is not referable to the genus *Peltosaurus;* it is here placed in a new genus, *Pancelosaurus*. *Pancelosaurus piger* differs in a great number of characters from *Peltosaurus granulosus*, the genotypic species. (1) *Pancelosaurus piger* has a sculpture consisting of irregularly-arranged pits and ridges on its body osteoscutes as well as on the osteoscutes fused with the cranial elements, in strong contrast with the raised tubercular sculpture of *Peltosaurus granulosus*. (2) The epidermal scale impressions on the frontals and parietals are also markedly different. On the frontal bones of *P. piger* the frontoparietals are widely separated, whereas in *P. granulosus* the same two scales are in broad contact. On the parietal bone in *P. piger* the interparietal impression is very large, whereas the occipital is small; the two impressions are nearly the same in *P. granulosus*. (3) The frontals are paired in the Cretaceous form,

whereas the same bones are fused in *P. granulosus*. (4) The rostral body of the premaxilla in the former is much more extended laterally than in the latter. (5) While in tooth structure the two forms are not unlike, the morphology of the structures in the Meckelian fossa differs markedly in the two lizards. The fossa is widely open lingually in *Peltosaurus*, and the intramandibular septum is placed well forward, whereas in *P. piger* this same septum is close to the posterior margin of the dentary, and the Meckelian fossa is less open here. In *Peltosaurus* the ventral border of the septum is almost completely fused with the rest of the dentary; in *P. piger* this same septum has a free ventral border. There are also some other, minor, differences between individual skeletal elements of the two genera as noted in the comparisons.

These same skeletal comparisons indicate that not only is *Pancelosaurus piger* not referable to the genus *Peltosaurus*, but in a number of its known characters this early anguid resembles the Recent forms more than it does most of the Eocene and Oligocene fossil anguids.

In the morphology of a number of individual cranial elements—frontal, parietal, maxilla, and premaxilla—*Pancelosaurus piger* resembles most closely the Recent *Diploglossus*, but differs from this Recent form in structure of the osteoscutes and in having toothed palatal elements. The ophisaurs differ from the diploglossines in these same respects, and it is with *Ophisaurus* that *P. piger* has the greatest number of fundamental characters in common: (1) Paired frontals. (2) Same type of rectangular body osteoscutes; sculpture of cranial and body osteoscutes similar. (3) Palatines and pterygoids both toothed (vomers unknown). (4) Frontoparietal scales separated at the midline, the separation of these scales greater in *Ophisaurus* than in *P. piger*. (5) Palatine process of pterygoid in advance of maxillary process. Confirmation of the presence (suggested

below) of a premaxillary foramen in *P. piger* would be of great importance, but since this fossil is known only from isolated bones, only suggestions can be made. The rostral body of the premaxilla of *Pancelosaurus piger* has an elongated maxillary process. The premaxillary process of the maxilla is short and strongly forked, and a septomaxillary fossa is present internal to the facial process. All these features contrast with the situation in *Gerrhonotus*, which lacks a premaxillary foramen, and agree with *Diploglossus* and *Ophisaurus*, in which such a foramen occurs, suggesting that it was also present in *P. piger*. However, the lingual margin of the premaxillae of *P. piger* is damaged in all specimens, and it is in this area that the delicate processes extend toward the inner prong of the anterior forked end of the maxilla, forming a premaxillary foramen.

Some of the characters shared by *Pancelosaurus piger* and the extant ophisaurs, such as paired frontals and toothed palatal elements, are without doubt primitive for anguids as well as for other lizards. Separation of the left and right frontoparietal scales on the midline also appears to be primitive for anguids, as suggested by the presence of such a condition in the overwhelming majority of extant anguids, as well as in another early anguid fossil, the Eocene *Xestops vagans*. In the probable possession of a premaxillary foramen and in having rectangular osteoscutes, *Pancelosaurus piger* exhibits an intermediate position (similar to *Ophisaurus*) between *Gerrhonotus* and *Diploglossus*. Resemblances of individual cranial elements between *Diploglossus* and the fossil *P. piger* are much greater than resemblances between *Ophisaurus* and *Diploglossus*. McDowell and Bogert (1954, p. 117) made the statement that "the Galliwasps (diploglossines) appear to be the most primitive of the Anguinomorpha"; this statement is supported by this study in that diploglossines show the greatest resemblance in a number of cranial elements to *Pancelo-*

saurus piger. However, the osteoscutes of diploglossines are radically different from those of *P. piger,* which in this feature agree with the extant ophisaurs and *Gerrhonotus.*

The occurrence of *Gerrhonotus*-like and *Ophisaurus*-like osteoscutes in *Pancelosaurus piger* may indicate one of two possibilities: (1) That *P. piger* is already somewhat specialized toward the line leading to these Recent forms and perhaps also to the large Eocene and Oligocene fossil forms, and that diploglossines represent an early divergent line from all other known anguids. (2) A less likely possibility in the present state of our knowledge is that the diploglossine scute was derived from the *Pancelosaurus* type of osteoscute. I consider the first alternative the simplest and more probable, and refer *Pancelosaursus* to the Anguinae.

Among the large Eocene-Oligocene anguids, *Pancelosaurus piger* shows the greatest number of characters in common with *Xestops vagans.* These two forms agree (1) in the arrangement of fronto-parietal scale impressions on the frontals, (2) in having paired frontals, and (3) in having toothed palatines. The osteoscutes are also somewhat similar in regard to general shape and in their beveled lateral edges, but the osteoscutes of *X. vagans* also show indications of lateral suturing. The osteoscutes of the two fossils differ in sculpture as well, and those of *X. vagans* bear keels.

The size of the isolated bones of *Pancelosaurus piger* suggests a lizard with a skull about 30 mm long. The vertebrae of *P. piger,* with their raised, rounded midventral area suggest a limbed rather than a limbless anguid (in the latter the centrum is markedly flattened ventrally), and this is substantiated by the presence of numerous limb bone fragments at the Bison Basin locality that are almost certainly referable to *P. piger.*

The type specimen (PU No. 14565) of *Peltosaurus jepseni* (Gilmore, 1942) now consists of only a posterior portion of the parietal bone and a body osteoscute. The maxilla associated with the type material and described by Gilmore (1942, p. 162) is now lost or misplaced. The osteoscutal crust covering the type parietals bears a sculpture consisting of low irregular ridges and pits and identical to that of *Pancelosaurus piger,* but in strong contrast to the granular ornamentation of *Peltosaurus granulosus* and *P. abbottii.* The small but wide occipital scale impression on the osteoscutal crust of *P. jepseni* is also in agreement with that of *P. piger,* but, again, differs from the elongate, relatively narrow, occipital scale impression of the peltosaurs. The osteoscutes are identical with those found in *P. piger.*

The type material of *Peltosaurus jepseni* is now supplemented by a nearly complete parietal, toothed pterygoids, and numerous jaw elements from the type locality. All the known skeletal elements of this form resemble these same elements of *Pancelosaurus piger,* and there is little doubt that the generic affinities of "*Peltosaurus jepseni*" are with *Pancelosaurus.* Even though the lizard remains referred to "*Peltosaurus jepseni,*" as well as those described above from the Bison Basin sediments in Wyoming, are of Tiffanian (late Paleocene) age, there is no indication of specific distinction in the morphology of these remains from those of the late Cretaceous *Pancelosaurus piger. Peltosaurus jepseni* is therefore included here in the synonymy of *Pancelosaurus piger.*

Summary. (1) The earliest known fossil anguid is from the Upper Cretaceous Lance Formation and was questionably referred by Gilmore (1928) to the genus *Peltosaurus.* The Cretaceous form has little in common with the genotype from the Oligocene, and is here placed in a new genus *Pancelosaurus.*

(2) *Pancelosaurus piger* shows greater resemblances to Recent anguids than to the large Eocene-Oligocene forms in size
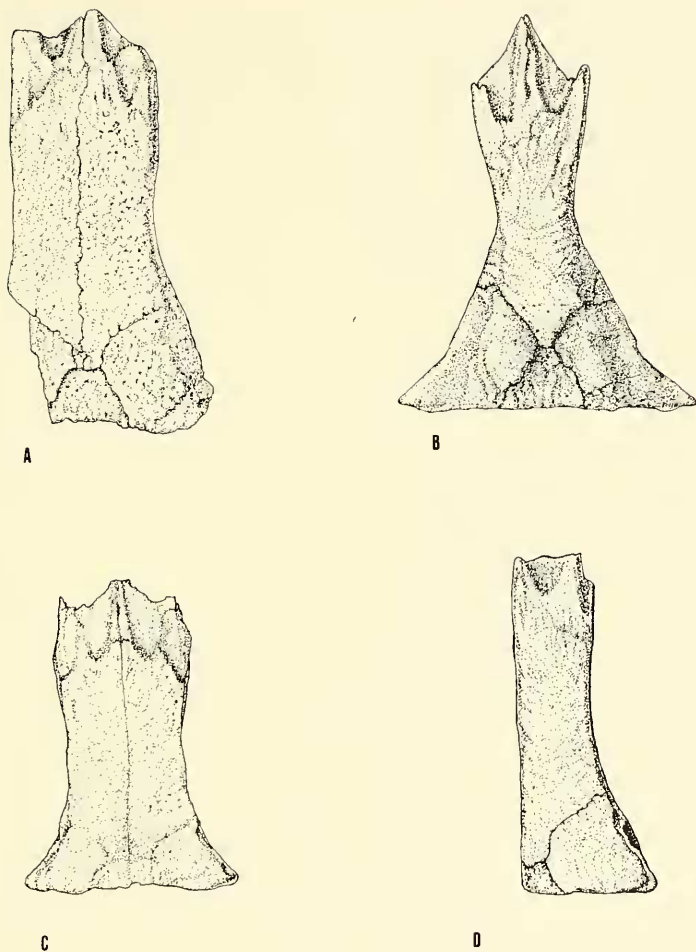
Figure 12. Frontals of recent and fossil anguids in dorsal view. A, *Pancelosaurus piger*, n. gen., (Bison Basin), MCZ 3496; B, *Gerrhonotus liocephalus*, Recent, MCZ 24518; C, *Diplaglassus hewardii*, Recent, MCZ 7356; D, *P. piger* (Hell Creek Formation, Montana), MCZ 3499. Note close resemblance between A and C. All × 4.

and arrangement of epidermal scales and in osteoscutal sculpture.

(3) The diploglossines exhibit a number of apparently primitive cranial characters, as indicated by the close resemblance between their individual skeletal elements and those of *Pancelosaurus piger*.

(4) The osteoscutes of *Pancelosaurus piger* are essentially the same as those found in *Gerrhonotus* and *Ophisaurus*, and unlike those of *Diploglossus*.

(5) *Pancelosaurus piger* exhibits the greatest number of fundamental characters in common with *Anguis* and the ophisaurs, and is referred to the subfamily Anguinae.

(6) Among the large early Tertiary anguids, *Pancelosaurus piger* resembles *Xestops vagans* most closely.

Pancelosaurus pawneensis (Gilmore 1928)

Xestops? pawneensis Gilmore 1928

Holotype. KU 1281. Gilmore based this species on the "median section of an articulated skull, with median part of attached

right ramus." The box bearing the above museum number now contains only a mesial portion of the right mandible, a small portion of the left maxilla, and fragments of the posterior portion of the right frontal.

Diagnosis. Similar in known characters and size to *Pancelosaurus piger,* differing from the latter in having recurved teeth with pointed apices that lack enameloid covering or striations.

Type locality. Sect. 28, T 11 N, R 53 W, 30 miles N of Sterling, Logan Co., Colorado.

Horizon. White River Formation (Cedar Creek beds), Middle Oligocene.

Original description. Gilmore (1928, p. 150) described this specimen as follows: "The teeth are closely placed subcylindric, with upper and lower teeth indistinguishable. In the maxilla eight and one-half teeth occupy a space of 5 millimeters. In size and lack of surface ornamentation these teeth bear a striking resemblance to those of *Exostinus serratus* found in this same region, differing chiefly in their more pointed apices.

"On account of the frontal bone being coossified with the overlying scutes it can not be determined whether the frontals were distinct or not. The granular surface ornamentation is similar to that in *X. vagans,* and the frontoparietal scutes are separate on the mid line as in that species. The post- and prefrontals are perhaps less widely separated above the orbits in this new species. Between the orbits the frontal bone has a width of 5 millimeters.

"The orbits are large, subcircular in outline; nasals distinct. That portion of the palate still preserved, consisting of articulated palatines and vomers, bears a strikingly close resemblance to the palatal region of *Gerrhonotus,* and apparently indicates its anguid relationship. The vomers are in close apposition in front, separated by a fissure posteriorly, the anterior ends slightly excavated on their inferior surfaces. Palatines descending from

the plane of the vomers; vomerine and maxillary processes subequal in size. Palatine foramen of good size. The presence of a single small body osteoderm with the skull is all that we know of the dermal covering. Its external surface is sparsely pitted, and it shows the usually smooth overlap surface at one end."

Redescription of the remaining type material. The frontal fragment, consisting of the right posterior corner of this bone, displays a sculpture pattern consisting of irregularly arranged pits and ridges, and not a "granular. . .ornamentation," as Gilmore described it. On the osteoscutal crust the outline of a large frontoparietal scale is imprinted. The postfrontal incision reaches to almost the anterior extremity of the above scale imprint. The lateral corner of the frontal fragment is devoid of osteoscutal crust.

The right mandibular fragment contains four teeth, the crowns of which are badly damaged. On the lingual surface the anterior inferior alveolar foramen is bordered by the dentary above and the splenial below. The anterior mylohyoid foramen is surrounded by the splenial alone. The anterior portion of the preserved splenial bone is ventral in position.

The maxillary fragment contains eight complete teeth and one fragmentary one. Three of the teeth are small and are apparently replacement teeth just moving into position. The crowns of the larger teeth are well preserved, and are unstriated with pointed recurved transparent apices. The apices are directed posterolingually. The shafts of the teeth are also slightly inclined posteriad. The facial process of the maxilla is not preserved, but the dorsal surface of the dental shelf bears a channel leading to the infraorbital foramen.

The fragments of the type specimen and Gilmore's original description are beautifully supplemented by two specimens from Round-top, Dawes Co., Nebraska (Lower Brule Formation, Middle Oligocene), FMNH P27236 and P27235, which

TABLE 1. ANGUID SUBFAMILIES AND REFERRED GENERA OF VARIOUS AUTHORS DISCUSSED IN TEXT.

COPE 1900	McDOWELL & BOGERT 1954	HOFFSTETTER 1962	THIS PAPER
Anguinae	Anguinae	Anguinae	Anguinae
Anguis	*Anguis*	*Anguis*	*Anguis*
Ophiodes		*Celestus*	*Ophisaurus*
	Gerrhonotinae	*Diploglossus*	*Pancelosaurus*
Ophisaurinae		*Ophiodes*	
	Abronia	*Sauresia*	Gerrhonotinae
Dopasia	*Coloptychon*	*Wetmorena*	
Hyalosaurus	*Gerrhonotus*		*Abronia*
Ophiodes	(including	Gerrhonotinae	*Coloptychon*
Ophisaurus	*Barisia* and		*Gerrhonotus*
Pseudopus	*Elgaria*)	*Abronia*	(including
	Ophisaurus	*Coloptychon*	*Barisia* and
Gerrhonotinae	(including	*Gerrhonotus*	*Elgaria*)
	Dopasia,	(including	*Paragerrhonotus*
Barisia	*Hyalosaurus,*	*Barisia* and	
Gerrhonotus	and *Pseudopus*)	*Elgaria*)	Diploglossinae
(including	*Placosauriops*	*Glyptosaurus*	
some species	*Placosauroides*	*Melanosaurus*	*Diploglossus*
later referred		*Ophipseudopus*	(including
to *Abronia*)	Diploglossinae	*Ophisauriscus*	*Celestus* and
		Ophisaurus	*Sauresia*)
Mesaspis	*Celestus*	*Parapseudopus*	*Ophiodes*
	Diploglossus	*Peltosaurus*	*Wetmorena*
Diploglossinae	*Ophiodes*	*Placosauriops*	
	Sauresia	*Placosauroides*	Glyptosaurinae
Celestus	*Wetmorena*	*Placosaurus*	
Diploglossus	*Xestops*	*Xestops*	*Arpadosaurus*
Microlepis			*Glyptosaurus*
Onida	Glyptosaurinae		*Melanosaurus*
Panolopus	*Glyptosaurus*		*Paraxestops*
Sauresia	*Placosaurus*		*Peltosaurus*
	Placotherium		*Placosauriops*
			Placosauroides
			Placosaurus
			Xestops

agree with the above description and the remaining type fragments in every detail.

FMNH P27236 (Pl. 1). A skull with mandibles and with most of its parts preserved anterior to the parietal suture. The snout is slightly damaged, and the premaxilla is missing.

Description. The frontals are paired, and the osteoscutal crust on the dorsal surface is sculptured with irregular pits and ridges. The right frontoparietal scale impression does not reach the metopic suture, but is separated from it by a small interparietal impression. That portion of the left frontal that bears this same scale impression is not preserved. The nasal bones are distinct. The prefrontal bone is present and separated from the postfrontal incision. The maxilla has a well-developed facial process. Posterior to this process the maxilla is twisted labially.

The maxilla is nearly complete, with only its most anterior extremity missing. Spaces and preserved teeth indicate a tooth count of 13–14. The teeth are essentially as described for the holotype. In the labial contact between dentary and postdentary bones the surangular is well in advance of
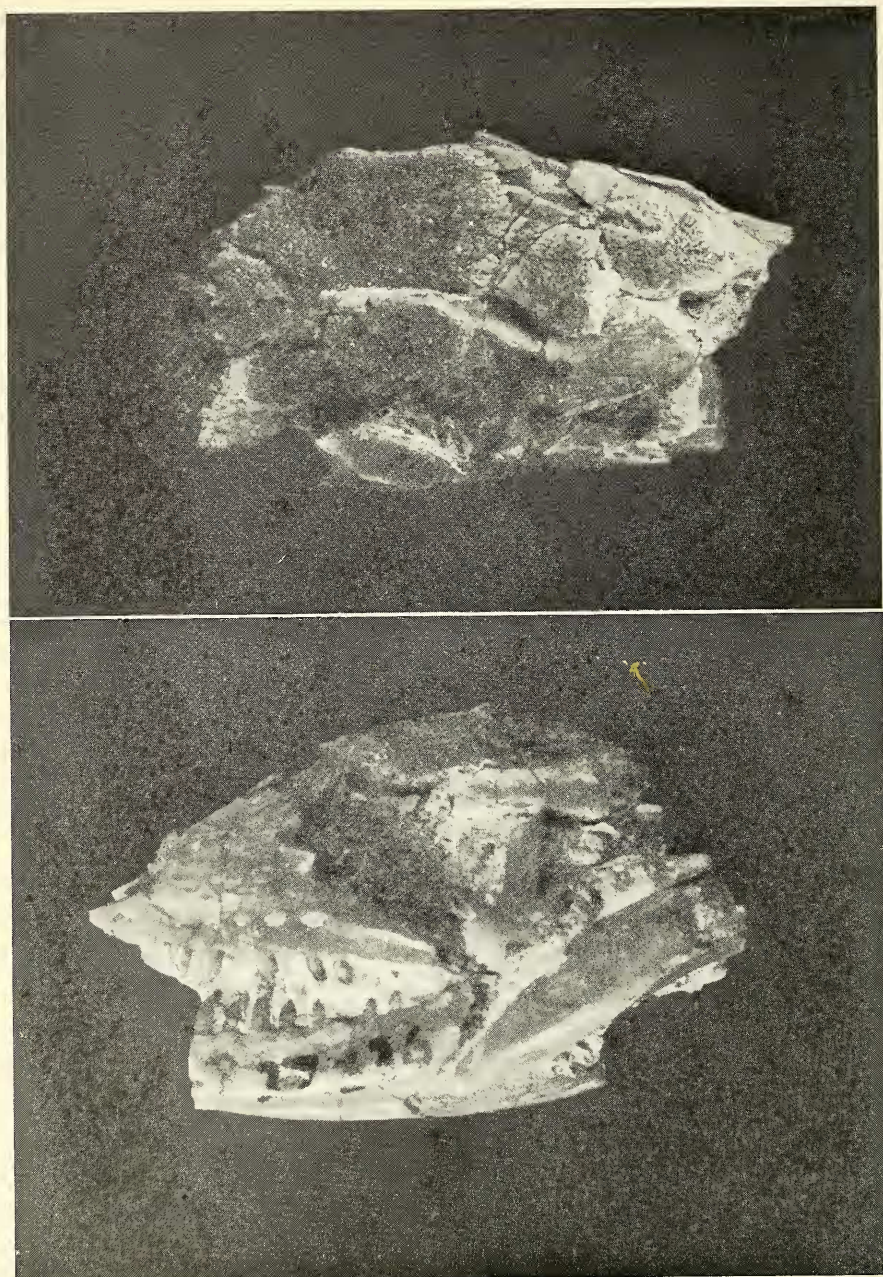
Plate 1. *Pancelosaurus pawneensis*, n. gen., FMNH P27236. Top: Dorsal surface of skull, showing frontals; anterior to the right. Bottom: Left side of the same showing maxilla and mandible. Note pointed teeth. Both × 4. Middle Oligocene, Brule Formation, Nebraska.

the dentary process of the coronoid bone. The preserved portion of the dentary bears seven teeth and spaces for three.

FMNH P27235. The skull of an anguid lizard somewhat smaller than the above, with most of its preserved parts anterior to the frontoparietal suture. The premaxilla is missing, as in the previous specimen, but the palate is here exposed with vomers and palatines visible.

Description. The frontals are the same as described for the previous specimen. Anterior to the frontal bones on the right side a large prefrontal is present, and it was apparently in contact with the left prefrontal scute at the midline. The facial process of the maxilla is not in contact with the frontal bone. The palatines bear a patch of tubercular teeth, but no vomerine teeth are present. The tooth count as indicated by spaces and complete teeth is 13–14 for the maxilla.

Discussion. The type of sculpture on the cranial osteoscutes and the small size of this Oligocene anguid relate it to *Pancelosaurus piger*, rather than to the Eocene *Xestops* as Gilmore (1928) believed. It also differs from *Xestops vagans* in having pointed teeth. Its other known character-states, excepting teeth, are also in agreement with *P. piger* and include (1) unfused frontal bones, with left and right frontoparietal scales separated at the midline, (2) toothed palatines, (3) maxillary tooth count of about 13–14, (4) deep anterior incision on the frontal bone for the nasal, (5) general morphology of the individual cranial elements. The teeth are strikingly different in the two species: blunt and with striated crowns in *P. piger*, unstriated with pointed apices in *P. pawneensis*, indicating the specific distinctness of the latter.

It is interesting that *Pancelosaurus pawneensis* exhibits a labial contact between dentary and postdentary bones similar to that found in modern anguines, and distinct from that shown by its contemporaries *Peltosaurus* and *Glyptosaurus*, or Eocene *Glyptosaurus*, *Melanosaurus*, and *Xestops*.

In *P. piger* the dentary is disarticulated in all known Cretaceous specimens, but the dentary shape indicates that surangular and coronoid were approximately in line as in the glyptosaurines (MCZ 3688, 3689; Hell Creek Formation, Montana). This condition is confirmed by articulated late Paleocene specimens of *P. piger* (specimens formerly referred to *Peltosaurus jepseni*; USNM 16880, Montana and PU 17148, Wyoming). In this feature *P. pawneensis* is specialized toward the Recent anguines.

Xestops Cope 1873

Type species of the genus. Xestops vagans (Marsh 1872).

Geological range. The genus is only known with certainty from the Middle Eocene of North America.

Referred species. Only a single species, *X. vagans*, is recognized here (see below).

Xestops vagans (Marsh 1872)

> *Oreosaurus vagans* Marsh 1872
> *Dimetopisaurus wyomingensis* Hecht 1959

Holotype. YPM 541. The type material consists of the following disarticulated skeletal elements: frontals; three lower jaw fragments, two representing the major posterior portions of left and right dentaries, latter with portions of coronoid, surangular and splenial attached, the third fragment probably representing the anterior portion of the above right jaw fragment; a small portion of the right maxilla; pterygoid; numerous dermal body scutes and unidentified bone fragments. Since the type material consists of numerous disarticulated elements, the frontals are designated here as the lectotype (Fig. 13, a-b).

Horizon. Bridger Formation (Horizon B), Middle Eocene.

Type locality. Grizzly Buttes, Uinta County, Wyoming.

Revised description. The right and left frontals are suturally distinct. The left

Table II. Holotypes of North American Anguid Fossils Examined.

Dimetopisaurus wyomingensis Hecht 1959, AMNH 3819

Glyptosaurus sylvestris Marsh 1871, USNM 16523
    G. nodosus Marsh 1871, USNM 16520
    G. princeps Marsh 1872, USNM 16539
    G. rugosus Marsh 1872, USNM 16526
    G. sphenodon Marsh 1872, USNM 16524
    G. tuberculatus Douglass 1903, CM 707
    G. montanus Douglass 1908, CM 1050
    G. giganteus Gilmore 1928, CM 1471
    G. hillsi Gilmore 1928, USNM 6004
    G. donohoei White 1952, USNM 18317

Melanosaurus maximus Gilmore 1928, AMNH 5168*

Odaxosaurus obliquus Gilmore 1928, USNM 10751 (synonym of *Pancelosaurus piger*)

Peltosaurus granulosus Cope 1873, AMNH 1610
    P. abbottii, Gilmore 1928, FMNH 12861
    "*P.*" *piger* Gilmore 1928, USNM 10687 (*Pancelosaurus*, n. gen., see below)
    P. jepseni Gilmore 1942, PU 14565*

Xestops vagans Marsh 1872, USNM 16532
    X. gracilis Marsh 1872, USNM 16529
    X. lentus Marsh 1872, USNM 16531
    X. microdus Marsh 1872, USNM 16528
    X. minutus Marsh 1872, USNM 16530*
    X.? pawneensis Gilmore 1928, KU 1281*
    X.? piercei Gilmore 1938, USNM 13807

* Type specimen damaged or parts of it missing since original description.

frontal is almost complete, with only the anterior tip missing, but only about half of the right frontal is preserved. The posterolateral corners of both left and right frontals are missing. The roofing osteoscutes are fused to the frontals and the osteoscutal surface is sculptured with tubercular mounds. Grooves on the osteoscutal surface indicate the outlines of the epidermal scutes. The two large frontoparietal scutes are separated by the narrow, wedge-shaped impression of the interparietal. The posterolateral portion of the dorsal surface has a deep incision not covered by osteoscutes. In lateral view the postfrontal depression is small, but the prefrontal impression is extensive and closely approaches the former, indicating that the prefrontal formed the greatest portion of the dorsal border of the orbit. Olfactory processes are well developed, but do not meet ventrally.

The left dentary fragment represents the posterior portion and contains six teeth, the posterior one much smaller than the rest. Spaces for three missing teeth are also present. Some of the crowns are well preserved, exhibiting an anteroposteriorly compressed cutting edge sculptured with vertical striations. The teeth are relatively robust, with an almost uniform diameter along the entire shaft. The intramandibular septum is well developed, and its free ventral border ends under the last tooth. The position of the anterior inferior alveolar foramen is not determinable.

There are two lower jaw fragments, presumably representing the right jaw of the same individual. However, the two fragments do not fit together, and it is assumed that an intermediate piece of this jaw is missing. The larger jaw fragment is composed of the dentary, splenial, coronoid, and surangular. The dentary has six preserved teeth, again the last being much smaller than the rest. The crowns are poorly preserved. The dentary extends posteriad, between coronoid and surangular, to the anterior supra-angular foramen. On the labial surface of the mandible the anterior extremities of the coronoid and the surangular are in the same vertical plane. The splenial is badly damaged. The smaller and more anterior portion of the right dentary has seven partially preserved teeth and space for one. None of the tooth crowns is preserved.

The right maxillary fragment contains two complete teeth and fragments of two others.

The pterygoid fragment is almost entirely covered with small tubercular teeth. The patch at its widest point is about 12 teeth wide.

The body osteoscutes are longer than wide, rectangular, and covered with tuber-
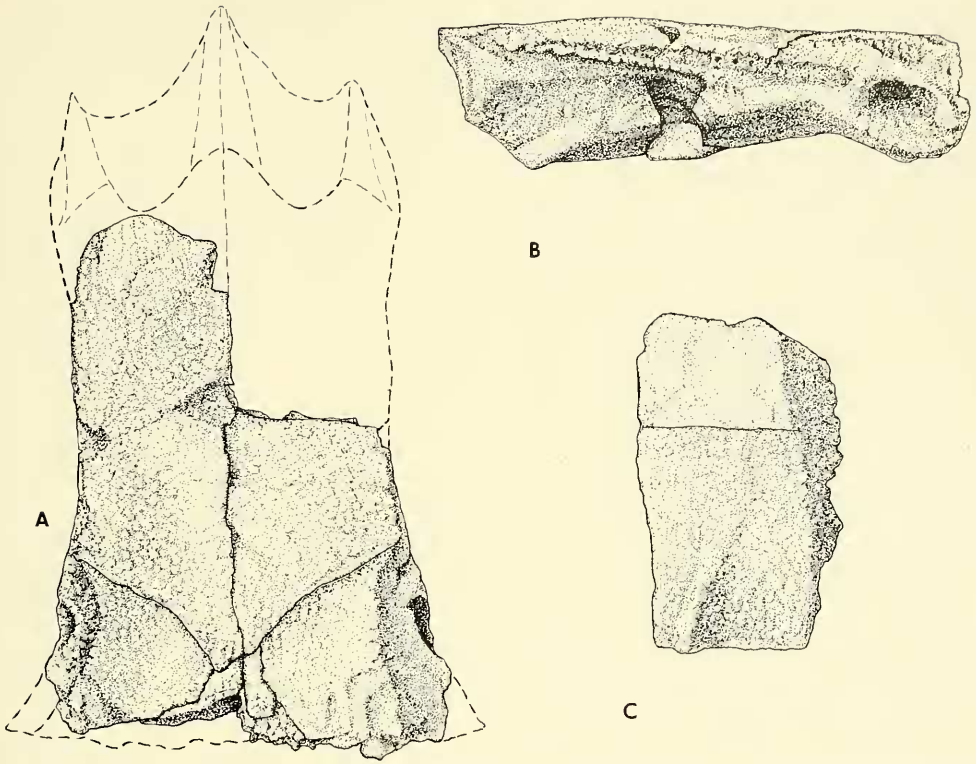
Figure 13. *Xestops vagans*, USNM 16532, holotype frontals and osteoscute. A, left lateral view of frontals; B, the same, dorsal view; C, lateral body osteoscute. All × 4. Frontals restored partially on basis of AMNH 3919. Middle Eocene, Bridger Formation, Wyoming.

cular mounds as in the frontals, but with smooth anterior gliding surfaces indicating the area overlapped by the preceding scute. The gliding surface occupies about one-third of the total length of the entire scute. A lateral overlap is also indicated between adjoining scutes by ventral and dorsal oblique surfaces along the lateral edges. Jagged lateral edges suggest some degree of suturing between osteoscutes. The scutes are keeled, the keels asymmetrical in all but middorsal scutes and extend from an anterior mesial position to the left or right corner, depending on the side of the animal from which they come.

Discussion. The type of *Xestops vagans* consists of isolated fossil elements and the danger always exists that more than one individual may be represented. However, the remains do not include any extra elements that would indicate the presence of more than one individual, and the size of the bones is also consistent with the assumption that they all represent a single individual.

The type frontal was figured by Gilmore (1928, p. 145), and this figure was copied by McDowell (1954, p. 116, fig. 37). Gilmore figured the outline of the frontoparietal scutes, but did not recognize the interparietal epidermal scute impression, giving the figure a pathological appearance. The type, however, clearly shows a triangular interparietal scute impression separating the two frontoparietals at the midline (Fig. 13b).

The frontals of *Xestops vagans*, in having a metopic suture and relatively straight orbital borders, resemble those of the Upper Cretaceous *Pancelosaurus piger* as well as those of Recent diploglossines, ophisaurs, and *Anguis*. The borders of the type frontals appear even straighter as a result of the missing posterolateral corners, which ordinarily expand laterally at the frontoparietal suture. The epidermal scutellation, as indicated on the osteoscutal surfaces, also resembles the above Recent forms, but in *Xestops* and P. *piger* the frontoparietal scutes approach one another somewhat closer at the midline than in Recent anguids. The sculpture of the osteoscutes is, however, very different from that in the above forms, and is identical with that of *Peltosaurus granulosus, Melanosaurus*, and *Glyptosaurus*. In tooth structure *Xestops* also resembles P. *granulosus* and *Melanosaurus* and to a lesser degree *Pancelosaurus piger*. The labial contact of the surangular, coronoid, and angular with the dentary also resembles that found in the above fossils and *Glyptosaurus* with the exception of P. *piger*, but in P. *granulosus* the labial dentary process of the coronoid is slightly in advance of the surangular, whereas in the rest of the above the anterior extremities of these bones are in line, as in *Xestops*. Correlated with this arrangement of bones, the dentary extends posteriad below the coronoid to the anterior supra-angular foramen in these fossil forms.

The body osteoscutes of *Xestops vagans* have beveled lateral edges, indicating that they overlapped laterally as well as anteroposteriorly. This feature and the straight orbital borders of the frontals were utilized by McDowell and Bogert (1954) to refer *Xestops* to the Diploglossinae. The thick, well-ossified, rectangular osteoscutes of X. *vagans* are unlike the thin, subcircular osteoscutes of Recent diploglossines. They bear the closest resemblance, among the Recent forms, to osteoscutes of the ophisaurs, especially those of *Ophisaurus apodus*. The osteoscutes of X. *vagans* also resemble those of *Melanosaurus, Glyptosaurus*, and *Peltosaurus granulosus* in sculpture, in general outline, and in heavy ossification. The osteoscutes of the latter are somewhat thinner than those of *Xestops vagans*. The lateral beveled edges, although very pronounced, are not unique to *Xestops*. The osteoscutes of *Pancelosaurus piger* show pronounced beveled lateral edges, and the osteoscutes of P. *granulosus* also overlapped to a lesser degree. Some indication of lateral overlap is present in a number of other anguid fossils (see also Hoffstetter, 1962, p. 154, fig. 3).

The characteristic pattern of the labial contact of dentary and postdentary bones of the mandible, similar teeth, and a tubercular sculpture of the osteoscutes, relate *Xestops vagans* to the large Eocene and Oligocene fossil forms *Melanosaurus, Arpadosaurus, Glyptosaurus*, and *Peltosaurus*. The epidermal scale imprints on the osteoscutal crust of the frontals of *Xestops* is similar to that found in *Pancelosaurus piger*, and the unfused condition of these bones suggests that X. *vagans* is structurally the most primitive member among the above-listed Eocene and Oligocene fossil genera, and the one most closely related to *Pancelosaurus*.

Hecht (1959, pp. 132–134) described *Dimetopisaurus wyomingensis* from the Middle Eocene Bridger Formation at Tabernacle Butte, Wyoming. The holotype (AMNH 3819) consists of a nearly complete left frontal. On comparison, the type frontals of *Dimetopisaurus wyomingensis* agree in every observable detail with the holotype of *Xestops vagans* (which was unavailable to Hecht at the time of his description). The two frontals agree in total length, osteoscute sculpture, epidermal scale impressions, general shape, and shape of the prefrontal and postfrontal impressions, as well as their distance from one another. The assumption that D. *wyomingensis* is a synonym for X. *vagans* is further strengthened by the fact that Hecht recognized osteoscutes of *Xestops*

from the same sediments from which he described *D. wyomingensis*. Both *X. vagans* and *D. wyomingensis* are known only from Middle Eocene deposits. *D. wyomingensis* is here considered a synonym of *Xestops vagans*.

Only the single species *Xestops vagans* can be recognized with certainty. Four additional Bridger Formation species of *Xestops* were described by Marsh (1872); these are reviewed below. Gilmore (1928) described *Xestops pawneensis* (White River Formation, KU 1281, Gilmore, 1928), which has already been referred above to the new genus *Pancelosaurus*. The holotype of *X. piercei*, USNM 13807, Wasatch Formation (Gilmore, 1938), is a poorly-preserved partial skull, lacking the diagnostic frontals, parietals, and osteoscutes; it is therefore a *nomen nudum*. Gilmore's generic assignment rested on laterally-beveled osteoscutes, and specific distinctness was based on a pitted rather than tubercular osteoscutal sculpture. The osteoscute is heavily worn, and its present sculpture is probably the result of wear. The specimen may be *Xestops vagans* or it may be another anguid.

All of the Marsh holotypes, except that of *X. vagans*, are fragmentary and defy generic assignment, and in one case the type material clearly contains nonanguid remains. The type of *Xestops gracilis* (USNM 16529) consists of four keeled, elongated osteoscutes and may represent those of the tail region of *X. vagans*. The dentary associated with the osteoscutes is not anguid, for the Meckelian groove is closed by bone. The type of *X. lentus* (USNM 16531), consists of two caudal vertebrae with chevrons apparently fused to the centrum. The type species material lacks caudal vertebrae, so that generic reference of caudal vertebrae cannot be regarded as valid, although they would not be an acceptable type in any case. In the original Marsh description of the type of *X. minutus* (USNM 16530), and also noted by Gilmore (1928), a maxilla and a dentary are men-tioned. The dentary has either been lost or misplaced. The tiny maxillary fragment contains four teeth that resemble those of *Gerrhonotus* rather than those of *Xestops*, but once again the specimen is too fragmentary for positive generic identification. *X. microdus* (USNM 16528) is represented by a dermal headscute similar to the ones found in *Glyptosaurus*, and a dentary fragment with three complete teeth bearing striated crowns with enameloid covering. The teeth are very slender, with a very strong subdental shelf. The type material also contains a fragmentary vertebra. Here again I can see no reason to assign this fragmentary material to the genus *Xestops*. The cranial osteoscute would indicate a more likely glyptosaurid affinity, though the other material is unidentifiable. *X. gracilis*, *X. lentus*, *X. minutus*, and *X. microdus* are all *nomina nuda*.

Hoffstetter (1962b) has described a very closely related form, *Paraxestops*, from the late Eocene of Switzerland, that will be discussed in a study in progress (Estes and Meszoely, ms.).

Peltosaurus Cope 1872

Type species of genus. Peltosaurus granulosus Cope 1872.

Geological range. Only known with certainty from the Oligocene of North America. Various jaw elements have been referred to this genus, but in view of the great similarities among the teeth of a number of anguid genera of the Eocene and Oligocene, these identifications are very possibly erroneous.

Referred species. Peltosaurus granulosus and *P. abbottii*.

Peltosaurus granulosus Cope 1872

Holotype. AMNH 1610. The type material consists of the following disarticulated skeletal elements: portion of frontals, parietal, premaxilla, greater portions of left and right mandibles, small fragments of left maxilla, jugal, osteoscutes, and verte-

TABLE III. *PANCELOSAURUS PIGER* SKELETAL ELEMENTS EXAMINED FROM VARIOUS LOCALITIES.

	LANCE FORMATION (LATE CRETACEOUS) WYOMING	HELL CREEK FORMATION BUG CREEK ANTHILLS (LATE CRETACEOUS) MONTANA	BISON BASIN LOCALITY TIFFANIAN (LATE PALEOCENE) WYOMING
Dentaries	9	50 +	12
Maxillae	6	50 +	4
Premaxillae	0	1	3
Frontals	3	2	23
Parietals	2	4	4
Pterygoids	0	0	7
Palatines	0	0	4
Osteoscutes	7	40 +	100 +
Vertebrae	5	10	100 +

brae. The type material also includes two blocks of matrix containing osteoscutes and fragments of postcranial elements.

Type locality. Cedar Creek, Logan Co., Colorado.

Horizon. Cedar Creek beds, White River Formation, Middle Oligocene.

Gilmore (1928, pp. 122–135) described the skeleton of *Peltosaurus granulosus* in great detail. Most of his observations are correct, but the emphasis placed by him on certain cranial characters differs from mine, and there are also some corrections and new observations to be added to his description. Not all the skeletal elements of *Peltosaurus granulosus* are redescribed here, but only those that are in my view diagnostic, those that were described erroneously, or those about which my observations differ from those of Gilmore. The description is based on all *Peltosaurus* material available to me (Table IV).

Revised description. The frontals are fused, with gently concave borders. The greater part of the frontals is covered by osteoscutes that are fused to the frontal bones. The osteoscutal crust is covered by raised tubercles. The outline of two large frontoparietal scales is impressed upon the osteoscutal surface, extending anteriad somewhat less than one-half the entire length of that surface. The two fronto-parietal impressions make strong medial contact with one another, almost excluding the single medial interparietal scale im-

pression from the frontal bone. The latter is a tiny wedge-shaped impression confined to the medioposterior border of the frontal bone. The posterolateral corners of the frontal are devoid of osteoscutes. The anterior end of the frontal bears two deep, wedge-shaped depressions for the insertion of the nasal bones. Next to these depressions the frontal is also devoid of osteoscutal crust, indicating overlap of this area by the prefrontal osteoscutes. The lateral surface bears two deep incisions: a posterior small one for the postfrontal and an anterior large one for the prefrontal bone. The two incisions are widely separated. The ventral surface is smooth, shows no suturing where the two frontals are fused, and bears the olfactory processes.

The parietal table is wider than long, with a small medial notch in the back. The osteoscutal crust covers more than one-half of the anterior surface of the parietal table, and is covered with the same tubercular mounds as the frontals (Pl. 2). Grooves indicate the impression of paired lateral parietals, a single, medial, wedge-shaped interparietal, and occipital epidermal scales. The latter two are approximately the same size, with the interparietal impression being slightly larger; this impression also bears the parietal foramen. The interparietal impression is relatively much narrower than in the Recent anguids. The temporal wings are expanded.

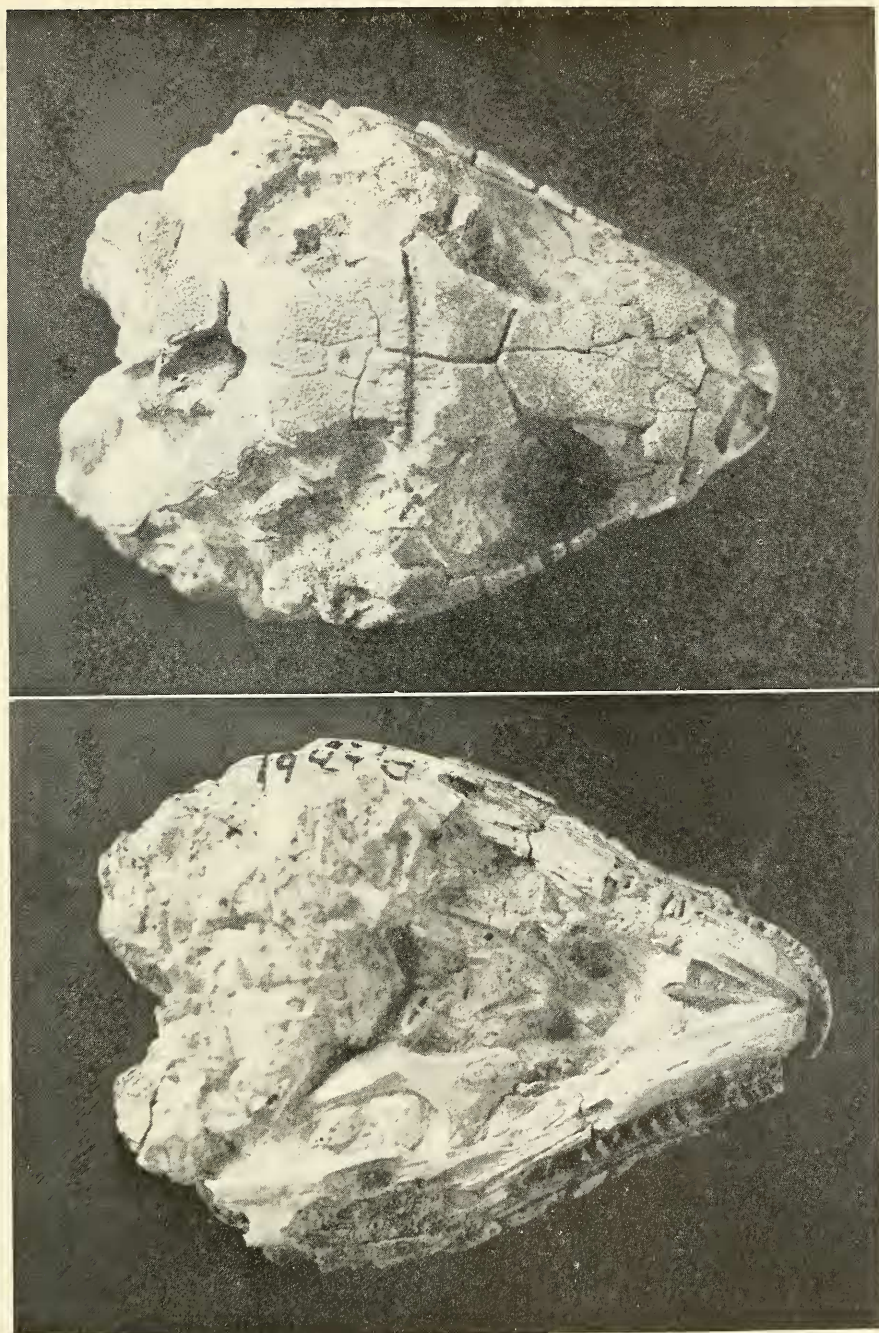On the ventral surface (Fig. 16d) a

Plate 2. *Peltosaurus abbottii*, FMNH P12861, holotype skull. Above: dorsal view of skull. Below: Ventral view of same. About × 2. Note wide pterygoid on the figure below. Oligocene, White River Formation, South Dakota.

troughlike depression leads to the parietal fossa, which is located at the apex of a triangular area enclosed by the converging anterior ridges. The parallel raised borders of the trough are formed by the posterior extension of the anterior ridges. The parietal fossa is an anteriorly-directed, slanted pit. Less prominent posterior ridges are present, extending into the temporal processes of the parietal.

No premaxillary foramen is present at the lateral union of maxilla and premaxilla.

The surangular, articular, and prearticular are indistinguishably fused in the mandible. The anterior extremities of the surangular and angular in labial view are set posteriad of the well-developed anterior coronoid process. Labially, the dentary contacts the anterior supra-angular foramen in about half of the specimens, but is excluded in the others. The distance between the anterior extremity of the surangular and the anterior tip of the dentary is nearly the same as from the former point to the posterior limit of the dentary. The latter distance is slightly greater. A small dorsal process of the dentary extends posteriad over the leading edge of the coronoid. On the lingual surface both dentary and splenial are involved in the formation of the anterior inferior alveolar foramen, which is under the fifth and sixth teeth from the rear (Fig. 17a).

The disarticulated dentary (Fig. 10d) exhibits a Meckelian fossa that is ventral anteriorly and extends to the tip of the dentary. The intramandibular septum is fused ventrally with the rest of the dentary. The septum is notched and the anterior extremity of the notch is under the fifth tooth, almost in line with the anterior inferior alveolar foramen. The dentary bears about 21 teeth. The most posterior tooth is the smallest, and the teeth increase in size to about the fifth tooth from the rear; after that they are subequal in size. The apices of the crowns of the teeth bear a cutting edge that is set almost parallel to the long

axis of the mandible but directed at an anteroposterior angle. The crowns bear striations set at a right angle to the cutting edge, and lack a dark enameloid covering. Some of the crowns are slightly expanded in a fan-shaped fashion in an anteroposterior direction.

The occipital condyle was described by Gilmore (1928) as follows: "The occipital condyle is reniform and relatively small as in *Gerrhonotus* and *Ophisaurus*. It is presumed that the exoccipitals contribute to the formation of the condyle but the coalescence of the sutures does not permit of a determination of this fact." The fused condition as described by Gilmore exists in most of the specimens examined, but in a small specimen of *Peltosaurus granulosus* (FAM 42915) the occipital condyle is clearly tripartite. In this specimen the three bones contribute nearly equally to the condyle formation, with the basioccipital contributing a little more than either the left or right exoccipital.

The osteoscutes are unkeeled, rectangular, and are covered with raised tubercular mounds; the smooth gliding surface makes up about one-third the total length. The osteoscutes have well-defined oblique surfaces along their lateral edges, one dorsal and the other ventral, indicating prominent overlap between adjacent osteoscutes. A lateral fold was probably present (KU 1280).

In the literature dealing with *Peltosaurus granulosus* the concept that it is very closely related to the Recent *Gerrhonotus* is firmly entrenched. This may be the result of three factors: (1) the historical treatment of *Peltosaurus granulosus*; (2) little or no knowledge of the cranial anatomy of pre-Eocene anguid fossils; (3) the fused frontals found in *Peltosaurus*, which among the Recent forms, occur only in the gerrhonotines *Gerrhonotus* and *Abronia*; (4) gerrhonotines share a similar type of body scutellation with *Peltosaurus*.

Cope, who described *Peltosaurus granulosus*, referred this fossil to his family

Gerrhonotidae. Later, Gilmore (1928) described *Peltosaurus* in great detail and made frequent comparisons with *Gerrhonotus*, probably in part the result of his limited comparative material. He apparently had only two *Gerrhonotus multicarinatus* and three *Ophisaurus ventralis* skeletons, and so far as is known, no *Diploglossus* material. It also should be pointed out that his comparisons did not always show close resemblance between the skeletons of *Peltosaurus* and *Gerrhonotus*. Tihen (1949) also included *Peltosaurus* along with *Melanosaurus* in the limbed Gerrhonotinae. McDowell and Bogert (1954, p. 115), suggesting a close relationship between *Peltosaurus* and *Gerrhonotus liocephalus*, gave a list of characters common for these two forms: (1) large frontonasal in contact with frontal scute; (2) two frontoparietal scales in medial contact separating the frontal and interparietal scales; (3) maxilla and frontal bones in contact; (4) left and right frontals indistinguishably fused. These points will be considered below.

(1) A frontonasal and frontal scute contact is not unique to these two anguids, but also occurs in *Ophisaurus apodus* and *Diploglossus monotropis*. (2) It is true that in both *Peltosaurus* and *G. liocephalus* the frontoparietal scales are in contact, but in *G. liocephalus* this contact is narrow, with the scales just touching along their anterior border, whereas in *Peltosaurus* the two scales are in contact almost along their entire length. (3) Maxillofrontal contact is again not unique to the two forms, but occurs in the Recent *Diploglossus* as well as in *Glyptosaurus*. (4) Fused frontals are found in *Gerrhonotus*, but occur also in *Melanosaurus* and some *Glyptosaurus*. It also may be pointed out that in *Peltosaurus* the postorbital and the postfrontal bones are fused, whereas they are always separate in *Gerrhonotus*, but fusion also occurs in some recent diploglossines.

The detailed study of *Pancelosaurus piger* presented above indicates the following conclusions in regard to *Peltosaurus*.

(1) The tubercular sculpture in *Peltosaurus* is not primitive, but aberrant, and is found only in Eocene and Oligocene forms and in the Recent *Gerrhonotus imbricatus*. (2) The strong medial contact of frontoparietal scales in *Peltosaurus* is not derivable from the relatively widely-separated frontoparietal scales of *Pancelosaurus piger*, without passing through a stage such as is found in modern *Gerrhonotus*, where these scales are barely touching. Thus this condition also appears to be aberrant. (3) The scalation of the parietal, as indicated by impressions, is again unlike Recent forms or *P. piger*. The interparietal and occipital scales are nearly equal in size in *Peltosaurus*, whereas in *Pancelosaurus piger* and the Recent forms the interparietal is much larger than the tiny occipital.

Thus, while perhaps *Peltosaurus* bears the most superficial resemblance among the large Eocene and Oligocene fossils to the Recent forms, its affinities are with the former group (*Peltosaurus, Xestops, Melanosaurus, Arpadosaurus, Glyptosaurus*), all members of which bear a granular tubercular sculpture on their osteoscutes absent in *Pancelosaurus piger*, which shares its pit-and-groove sculpture with the Recent forms. Also, the above large fossil anguids have a mandible in which the intramandibular septum is fused, and the anterior extremities of the coronoid and surangular bones are in a vertical plane on the labial surface (*cf*. Figs. 3, 17). In *Peltosaurus* (Fig. 17a) the coronoid extension is anterior to the surangular in contrast to Recent forms in which the latter bone always extends far anterior to the former. These conditions are not the result of size, since my comparative material includes some very small *Peltosaurus* skulls, the smallest measuring 29.9 mm, while the largest Recent skull, *Diploglossus occiduus*, measures 44.5 mm.

A number of pre-Oligocene fossil forms earlier referred to the genus *Peltosaurus* were referred above to the genus *Pancelosaurus*. The generic identification of *Pelto-*

AM 1610—skull and mandible fragments (type of *P. granulosus*)
  1652—skull and jaws, nuchal scutellation
  8138—skull and jaws, nuchal scutellation

FAM 42913—skull and jaws
  42915—skull and jaws
  42917—isolated frontals and parietals
  —— —isolated parietal

FMNH UR450—fragmentary skull and jaws of two individuals
  UR452—fragmentary right ramus
  UR453—left mandible
  UC391—skull, jaws, anterior body region, shoulder girdle
  UC1720—partial skull and jaws
  P12861—skull (type of *P. abbottii*)
  P25806—partial right mandible
  P27072—skull and jaws

KU 620—frontals, parietals, and isolated fragments
  1278—frontals and mandibular fragments
  1282—left dentary
  1283—mandible fragments
  1284—mandible fragments
  7654—many isolated fragments
  7661—skull, jaws, and fragments
  12957—frontals
  12958—mandible fragments
  12959—left maxilla
  12961—frontals
  12962—right dentary

U. Minn. VP-1511—skull, jaws, nuchal scutellation

USNM 1280—skull and jaws
  13870—skull and jaws
  15607—frontals

YPM 621—dentaries
  1061—skull and jaws

saurus from other than Oligocene deposits almost invariably has rested on tooth structure, even though Gilmore's observations should have been a warning against such actions. He wrote (1928, p. 146) describing the teeth of *Xestops vagans*: "As a whole they are practically indistinguishable from the teeth of *Peltosaurus*"; again (p. 142), in his description of *Melanosaurus:* "The dental formula of *Melanosaurus maximus* appears to be very similar to that of *Peltosaurus*"; and, again, in the description

of *Pancelosaurus* ("*Peltosaurus*") *piger* (p. 136): "The structure of the teeth, as mentioned above, is remarkably like that of *Peltosaurus*, but similar teeth are found in the very large *Glyptosaurus hillsi*." As clearly indicated from these quotes and confirmed by my observations, similar teeth are found in at least four fossil genera; tooth structure is therefore a very poor criterion for generic identification in fossil anguids.

Diagnostic cranial elements of *Peltosaurus*, such as frontals and parietals, are presently known only from Oligocene deposits, and there is therefore no good reason to recognize this genus from any deposits of any other age, although better material may in the future confirm time extensions in either direction.

Peltosaurus abbottii Gilmore 1928

Holotype. FMNH 12861, nearly complete skull.

Type locality. Cottonwood Creek, Washington Co., So. Dakota.

Horizon. Leptauchenia Zone (*Protoceras* beds), White River Formation, Upper Oligocene.

Gilmore (1928, p. 135) described this species as follows: "The great breadth of the skull back of the orbits, the more regular convex profile of the upper anterior half, and the presence of a large subtriangular frontonasal scute bordered on either side by a single large prefrontal scute appear to indicate its specific distinctness from *Peltosaurus granulosus.*"

Discussion. Peltosaurus abbottii is known only from a single specimen (Pl. 2). It is damaged in the cheek region on both sides, where the postfrontal articulates with the jugal, but these two bones are still in contact on the right side. Frontal and parietal bones are also slightly disassociated from one another at the frontoparietal suture, and the extremities of both of these bones are pressed downward by the sediment. These facts caution against placing much emphasis on the shape or breadth of the

skull, but certain other features exhibited by the specimen are perhaps indicative of a specific distinctness of this fossil from *Peltosaurus granulosus*. The frontonasal scute is broader, less elongate, and more triangular in *P. abbottii* than in *P. granulosus*. The interparietal scute incision, instead of being single, medial, and wedge-shaped, is paired and set to the side. The part of the pterygoid bone bearing the teeth is also relatively broader and more robust than in *P. granulosus*. Both pterygoids, as well as palatines, bear teeth as in *P. granulosus*. In all of its other known characters *P. abbottii* agrees with *P. granulosus*.

Although the differences discussed above appear to be minor, it should be pointed out that many diagnostic specific features used by modern herpetologists would probably not be preserved in the fossil forms. The species *P. abbottii* is recognized here with some hesitancy.

Melanosaurus Gilmore 1928

Xestops Camp (1923, p. 328).

Type species of the genus. Melanosaurus maximus.

Geological range. Known only from North American deposits of early Eocene age.

Referred species. The genus is represented by a single species, *Melanosaurus maximus*.

Melanosaurus maximus Gilmore 1928

Holotype. AMNH 5168. The type material consists of a block of matrix containing most of the compressed skull elements of one individual, and two smaller blocks containing vertebrae and osteoscutes. Isolated elements referred to this specimen include: greater portion of the right mandible, two maxillary fragments, a vertebra, and several osteoscutes.

Horizon. Wasatch Formation, "Above red-banded beds," Lower Eocene.

Type locality. Clark's Fork Basin, Big Horn County, Wyoming.

Revised description of the holotype. On the block containing the skull elements, the following bones are visible on the dorsal surface: frontal, parietal, jugal, supratemporal, quadrate, prefrontal, postorbital, postfrontal, coronoid, fused surangular-articular-prearticular, squamosal, and a small portion of the dentary.

Ventrally the following bones are visible: right dentary, vomers, palatines, pterygoids, basisphenoid, basi- and exoccipitals, left epipterygoid, right quadrate, and postfrontal.

Frontals: The frontals are fused; their lateral borders are gently concave in the orbital region. The maximum length of this bone is 29.2 mm and the maximum width along the frontoparietal suture is 22.8 mm. The roofing osteoscutes are coossified with the underlying bone, and are covered with tubercular mounds. Both lateroposterior corners are devoid of osteoscutal crust. Faint grooves are present on the surface and possibly indicate the outlines of two large frontoparietal and two smaller scales. The latter appear to be halfmoon-shaped and adhere to the anterior border of the frontoparietal. None of these is clearly defined, and thus they do not allow for positive statement regarding the epidermal scalation in this region.

Parietal: The parietal is covered with the same tubercular mounds as the frontals. Here faint grooves on the osteoscutal surface indicate the outline of interparietal and occipital epidermal scales. Both are relatively narrow and nearly equal in size. The former is triangular and bears the parietal foramen close to its posterior extremity. Two large, loosely-attached osteoscutes are present lateral to the occipital scale impression. The parietal table along the midline is 23.1 mm long. The proximal portion of the left supratemporal process bears a deep groove along its mesial border.

Jugal: The left jugal is roughly rectangular and is missing a large portion at the junction of the maxillary and the temporal processes. The posterior border of the temporal process is covered with minute ridges.

Squamosal: The squamosal is long, with a chord length of 30.0 mm.

Postorbital: The left postorbital now lacks the anterior portion, which was illustrated by Gilmore (1928, fig. 86) as covering the postfrontal.

Postfrontal: The left postfrontal is a tripartite bone with frontal, parietal, and well-developed jugal processes. The right postorbital located on the ventral surface bears a deep postorbital incision on its posterior border.

Quadrate: The quadrate has an extremely well-developed internal wing, which is exposed on the ventral surface of the block containing the skull elements.

Pterygoid: The pterygoids, palatines and vomers all bear teeth. In the first two the tooth patches are very large. The vomerine teeth form a narrow patch. Some of these minute teeth have sharp points and are recurved.

Occipital: The occipital region is badly damaged; very little of the natural surface is preserved.

Mandible: The anterior extremities of both dentaries are missing. The breakage on both occurred at nearly the same point, as shown by a tooth count of 11 in both dentaries. The right dentary contains seven complete teeth, the left dentary has only four; the rest of the teeth are fragmentary. The teeth are robust, with bluntly chisel-shaped crowns, which are compressed into slightly arched cutting edges, the main axis of which are parallel to the long axis of the jaw. Striations are present mostly at a right angle to the cutting edge. On the right mandible the contact of the dentary with the coronoid, surangular, and angular is visible, and the anterior extremities of the latter bones on the labial surface are in the same vertical plane. The anterior inferior alveolar foramen is between the dentary and the splenial. The dentary extends between the coronoid and the surangular to the anterior supra-angular foramen. The articular, surangular, and the prearticular are fused. The articular facet (preserved on the left mandible) is roughly elliptical, with the chorda tympani foramen posterior to the facet and the anterior articular foramen in front of the facet.

Maxilla: A medial portion of both maxillae is preserved. Both fragments contain spaces for seven teeth, but in both maxillae only five are complete. The teeth are essentially the same as described for the dentary. The anterior labial surface of both fragments is covered by osteoscutes.

Osteoscutes: The body osteoscutes have the same tubercular mounds as on the osteoscutes fused with the skull elements, and only about one-fourth the total length of the scute is occupied by the smooth gliding surface. The gliding surface and the sculptured surface are separated by a deep groove. The lateral edges of the osteoscutes have very well-developed suture surfaces. Only one osteoscute among the many in the type material is keeled.

Paratype. AMNH 5175. Isolated cranial and postcranial elements of a slightly larger individual than the holotype. The paratype material consists of the following disarticulated skeletal elements: frontals, parietal, premaxilla, right and left maxillae, right jugal, both quadrates, right dentary fragment, fused articular and surangular of the right mandible, other smaller mandibular fragments, vertebrae, and osteoscutes.

Locality. Big Horn Basin, Big Horn Co., Wyoming.

Horizon. Wasatch Formation, Lower Eocene.

Partial redescription. The paratype consists of isolated skeletal elements, and consequently the ventral surfaces of such diagnostic bones as the parietal and frontals are visible. The paratype material contains

a premaxilla and numerous body osteo-scutes, presumably from the posterior part of the body. Only those elements important to the discussion will be described below. For a more complete description the reader is referred to Gilmore (1928, pp. 138–144).

Frontals: The frontals are roughly tri-angular, with a maximum width of 30.2 mm and a maximum length of 34.5 mm. The corners of the frontals are rounded by wear, and the osteoscutal crust on the dorsal surface is badly eroded. A few pustules are present similar to the ones on the holotype. No impressions of epidermal scales are visible. Olfactory processes are present on the ventral surface and do not meet on the midline. Lateral prefrontal and postfrontal incisions are present and separated from one another by a narrow gap of 4.8 mm.

Parietal: Most of the parietal table of the paratype is preserved, but both of the supratemporal processes of this bone are missing. The parietal table is relatively elongate with gently concave lateral bor-ders. It has a maximum width of 28.0 mm along the frontoparietal suture and a maximum length of 24.5 mm. The osteo-scutal crust is badly eroded here as well, and no epidermal scale impressions are visible on the dorsal surface. On the ventral surface (Fig. 16a) the well-developed an-terior ridges converge posteriorly, forming a triangular area that encloses the parietal foramen and extends posteriad to the parietal fossa. The parietal fossa is an anteriorly-directed, slanted pit. The pos-terior ridges emerging from the supratem-poral processes converge on the anterior ridges at the level of the parietal fossa.

Premaxilla: The rostral body is relatively short and robust and bears a pair of prom-inent labial foramina. In anterior view the lateral margins of the rostral body are straight and converge from both sides on the nasal spine. There is no marked con-striction between the nasal spine and the rostral body. The rostral body has a chord length of 14.6 mm as measured between

the lateral extremities of the maxillary processes; there is a distance of 5.8 mm from its ventral margin to the point at which it gives off the nasal spine. The preserved portion indicates a tooth count of eight. Much of the morphology of this bone is concealed by hematite fused to the lingual surface.

Osteoscutes: The osteoscutes of the para-type display sculpture in which the tuber-cular mounds are arranged in concentric rectangles. The smooth gliding surface occupies a little over one-fourth the total length of the entire scute and is separated from the sculptured surface by a deep groove. The gliding surface is in the shape of a rectangular transverse band. The lat-eral surface of the scutes is highly irregular, indicating a high degree of lateral suturing between osteoscutes. A number of the osteoscutes bear keels, and all have nu-merous small foramina on their under sur-faces.

Discussion. Camp (1923) based his *Xestops* restoration on AMNH 5168. Gil-more (1928) referred this specimen to a new genus and species, *Melanosaurus maximus.* He noted that it resembled *Pelto-saurus granulosus* in having fused frontals with concave borders, and referred *M. maximus* to the family Anguidae. Mc-Dowell and Bogert (1954), while remark-ing that *Melanosaurus* in general shows, "a very specialized diploglossan morphol-ogy with much resemblance to such primitive Anguidae as *Gerrhonotus* or *Diploglossus*," referred *M. maximus* to the family Xenosauridae on the basis of the following six points:

1. The presence of an epiphysis of the paroccipital process as a sepa-rate ossicle.
2. The presence of an inner, wing-like conch on the quadrate.
3. Much dilated and sculptured post-orbital ramus of the jugal.
4. Coossification of the cranial osteo-derms with one another, as well as with the underlying bones.

TABLE V.   DISTRIBUTION OF SOME CHARACTER-STATES IN RECENT AND FOSSIL ANGUIDS.

	Pancelosaurus piger	Peltosaurus granulosus	Melanosaurus	Ophisaurus	Diploglossus	Gerrhonotus	Glyptosaurus
Frontals distinct	+	–	–	+	+	–	+(–)
Skull elements ornamented with tubercular mounds	–	+	+	–	–	–	+
Osteoscutes with prominent lateral overlap	+	+	–	+	+	+	–
Osteoscutes rectangular with transverse band-shaped gliding surface	+	+	+	+	–	+	+
Toothed pterygoids	+	+	+	+	–	+	+
Toothed palatines	+	+	+	+	–	–	+
Toothed vomers	?	–	+	+(–)	–	–	–
Frontoparietal scales separated by interparietals	+	–	?	+	+	+(–)	–

5. Lack of anterior expansion of the frontal, anterior to the orbital emargination.

6. Indications of a longitudinal crest along the temporal arch.

Each of these points will be considered below:

1. The exoccipital and prootic region of the holotype is damaged; the smooth surface bone layer is nowhere preserved in this region. It is only by comparison and by knowing the region where the prootic occurs that one can recognize this bone. The element referred to by Camp as the paroccipital appears as a separate piece, but may very well be a flake from the prootic region. Similar conclusions were reached by Hecht (1959). This small element bears little resemblance to the so-called "epiphysis" of the paroccipital of *Xenosaurus*. Estes (personal communication) has observed similar ossicles to those of *Xenosaurus* in some recent anguids (e.g. *Gerrhonotus multicarinatus*, MCZ 32250).

2. The holotype of *Melanosaurus maximus* shows a very large inner wing on the quadrate, as indicated by McDowell and Bogart, but the three *Xenosaurus grandis* skeletons in my possession show practically no development of this inner wing. However, the anguid *Ophisaurus apodus* has a well-developed internal wing of the quadrate, although it is smaller than that of *Melanosaurus*.

3. On the jugal of *Melanosaurus maximus* the postorbital and maxillary processes meet at a right angle, while the postorbital process of *Xenosaurus grandis* is strongly tilted caudad. The striations of the jugal are confined to the posterior and ventral border; similar striations also occur in some glyptosaurs, to which the jugals of *Melanosaurus* bear the closest resemblance. There is little resemblance between the jugal of *Melanosaurus* and that of *Xenosaurus*.

4. The coossification of cranial osteoderms with the underlying bones is an anguid character as well as a xenosaurid one. However, frontals of *Xenosaurus grandis* are covered with large raised osteoscutes that are coossified, and lines indicating the position of the epidermal scales

are absent. The skull roofing bones of *Melanosaurus* are covered by osteoscutes bearing a sculpture similar to that of *Xestops* or *Peltosaurus granulosus*, and the parietal osteoscutes clearly show the outline of interparietal and occipital epidermal scales characteristic for nearly all anguids, excepting *Glyptosaurus*.

5. The outline of the frontals (especially that of the paratype) bears an extremely close resemblance to that of some glyptosaurs (e.g. *G. rugosus*) and shows little resemblance to the emarginated, narrow frontals of *Xenosaurus grandis*. The frontal outline of the latter bears the closest superficial resemblance among Recent anguids to that of *Gerrhonotus liocephalus*.

6. It is difficult to comment on this statement, since it may refer to the supratemporal processes of the parietal or to the squamosal. It probably refers to the latter bone. The squamosal in *Melanosaurus* is very long and slender, whereas in *Xenosaurus* it is short and thick, with a posteriomesial weblike process that is in contact with the parietal, roofing over most of the upper temporal opening. The supratemporal processes of the parietal are also elongate, whereas in *Xenosaurus* these two are very short and stubby.

Gilmore (1928, p. 138) suggested that *Melanosaurus maximus* "has its nearest affinities with the genus *Peltosaurus*." There is a resemblance between *Peltosaurus granulosus* and *Melanosaurus* in that they both have fused frontals with concave orbital borders. The outline of the frontals of the holotype also resembles that of *P. granulosus*, while that of the larger paratype is closer to *Arpadosaurus* (see below) and *Glyptosaurus*. Sculpture type of the cranial osteoderms is essentially the same as in *P. granulosus*, but the same sculpture type also occurs in *Xestops*, *Arpadosaurus*, and *Glyptosaurus*. There is a similarity between the pattern of labial articulation between dentary and postdentary bones of *Melanosaurus* and *P. granulosus*;

but the similarity is even greater between *Melanosaurus* and *Glyptosaurus*. The heavy, sutured osteoscutes have a deep groove between the gliding surface and the sculptured surface and are very similar to those of *Glyptosaurus*; they resemble less the thin, essentially beveled scutes of *Peltosaurus granulosus*, which also lack the groove between gliding and sculptured surfaces. Also, with respect to size, *Melanosaurus* (especially the paratype) is in the range of the genus *Glyptosaurus*. *Melanosaurus* is more primitive than *P. granulosus* in having toothed vomerine bones and in having separate postorbital and postfrontal bones.

Thus, *Melanosaurus* shares a number of characters with *Peltosaurus granulosus*, but the majority are not unique to the two genera, being found also in other Eocene and Oligocene forms and thus may be regarded as specialized features characterizing a side line of anguid evolution. However, *M. maximus*, with regard to body scutes as well as size, shows a specialization toward the *Glyptosaurus* line. This specialization is not present in *P. granulosus*, whose geological occurrence is later (Oligocene) than that of the Eocene *M. maximus*. The affinities of *Melanosaurus* and *Glyptosaurus* are further discussed in the section dealing with *Arpadosaurus*.

Camp (1923) figured the reconstructed skull of *Melanosaurus* ("*Xestops*") *maximus* based on the holotype, and Gilmore (1928, p. 140) refigured Camp's reconstruction. In this figure, the postorbital is shown to exceed the postfrontal anteriorly, but examination of the holotype indicates a postorbital incision on the posterior border of the postfrontal bone, suggesting that the postorbital was excluded from the orbit, as in the glyptosaurs. It may be also pointed out that Gilmore's photographs of the vertebrae (pl. 23) and the jugal (pl. 24) do not represent the holotype (as indicated in the plate legend), but are skeletal elements of the paratype AMNH 5175.

Arpadosaurus gazinorum n. gen., n. sp.

Holotype. USNM 25826. The type material consists of disarticulated skull elements, osteoscutes, and fragments of vertebrae. The following skull elements have been identified: frontals, parietal, left and right dentary fragments, tip of the right maxilla, fragments of left and right palatines, right articular, and occipital condyle.

Horizon. Late early Eocene.

Locality. Twelve miles north of Big Piney, Wyoming; Wasatch Formation.

Diagnosis. A large anguid structurally intermediate between *Melanosaurus* and *Glyptosaurus* in scalation. *Arpadosaurus gazinorum* differs from the former in having an unusual epidermal scalation, as indicated by grooves on the frontal bone, and a less extensive patch of palatine teeth; from the latter it differs in that the head osteoscutes are not broken up into polygonal plates.

Etymology. *Árpád*—name of a 10th Century Hungarian leader who was lifted on shields into the air by his peers when they elected him as head of the seven tribes then inhabiting Hungary. The name refers to the shield-shaped fused frontal bones of the lizard. Greek, *sauros*—lizard. The specific name honors C. L. and Chester Gazin, who collected the specimen.

Description of skeletal elements. The frontals (Fig. 14) bear a dorsal metopic suture on the osteoscutal crust but are indistinguishably fused ventrally. They are roughly triangular in outline and short in relation to their width. Their maximum length is 32.8 mm, and they are 28.6 mm along the frontoparietal suture. The dorsal surface of the bone is covered by fused osteoscutes, which have a sculpture of small tubercular mounds. The frontal osteoscutal crust is traversed by numerous grooves, indicating the outlines of epidermal scales. A prominent groove traverses the frontal transversely about one-third the distance of total length of this bone from the frontoparietal suture. Posterior to the above
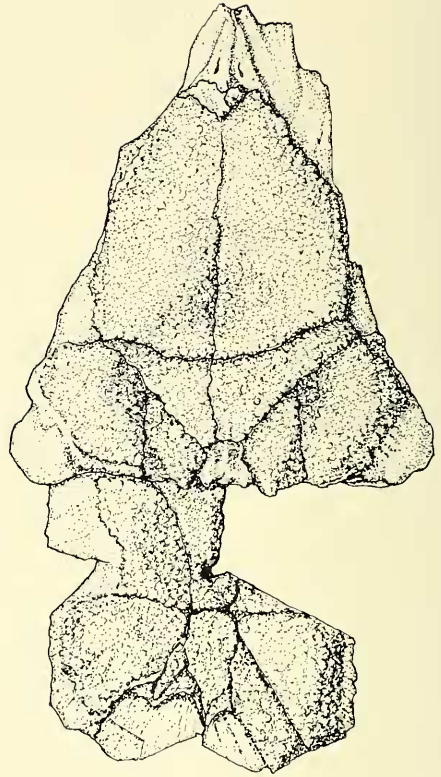

Figure 14. *Arpadosaurus gazinorum,* n. gen., n. sp., USNM 25826, holotype. Frontals and parietals, dorsal view, × 2. Early Eocene, Wyoming.

groove the dorsal surface of the frontal is further subdivided by several grooves. Two grooves, corresponding to the outline of frontoparietal scutes in other anguids, converge on one another toward the posterior midline, but are separated from one another by a small wedgelike area devoid of osteoscutes, presumably representing the interparietal epidermal scute area. The frontoparietal areas are again subdivided into unequal halves by a groove parallel to the metopic suture. On the lateral surface the prefrontal and postfrontal incisions are well defined. The prefrontal incision is the larger, occupying about two-thirds of the lateral surface of the frontal and separated from the postfrontal by only a 3 mm gap. The anterior extremities of the

TABLE VI. NEW WORLD FOSSIL RECORD OF THE ANGUIDAE.

Epoch	Gerrhonotinae	Anguinae	Glyptosaurinae	Diploglossinae
Pleistocene		*Ophisaurus ventralis* / *O. compressus*		*Diploglossus* spp. from Jamaica and the Dominican Republic (Etheridge, 1964, 1965)
Pliocene	*Paragerrhonotus* / *Gerrhonotus*	*Ophisaurus attenuatus*		
Miocene			Osteoscutes noted by Estes and Tihen, 1964	
Oligocene		*Pancelosaurus pawneensis*	*Peltosaurus abbottii* / *P. granulosus* / *Glyptosaurus* (3 species)	
Eocene	*cf. Gerrhonotus*		*Glyptosaurus* (8 species) / *Arpadosaurus gazinorum* / *Melanosaurus maximus* / *Xestops vagans*	
Paleocene		*Pancelosaurus piger*		
Late Cretaceous	*cf. Gerrhonotus*	*Pancelosaurus piger*		

olfactory processes are broken off. Posterior to these processes wedge-shaped impressions are present close to the posterior lateral extremity of the frontal.

The parietal (Figs. 14, 16c) is a quadrangular bone; most of its upper right quadrant is missing. The supratemporal processes are not preserved. Most of the dorsal surface of the parietal, except a small posterior area, is covered by coossified osteoscutes, which are covered with the same tubercular mounds as the frontals. Grooves indicating the outline of interparietal and occipital scutes are present.

The interparietal area is narrow and triangular, its apex directed posteriad and enclosing the parietal foramen. The occipital scale impression is subequal to the interparietal, but is subrectangular rather than triangular in shape. Large paired parietal scutes flank the interparietal area, and two similar ones flank the occipital. The occipital area mesial to the two large parietal scutes is also flanked by numerous elongate wedge-shaped irregular scutes.

On the ventral surface two anterior ridges converge posteriad to merge and continue as a single median ridge. The
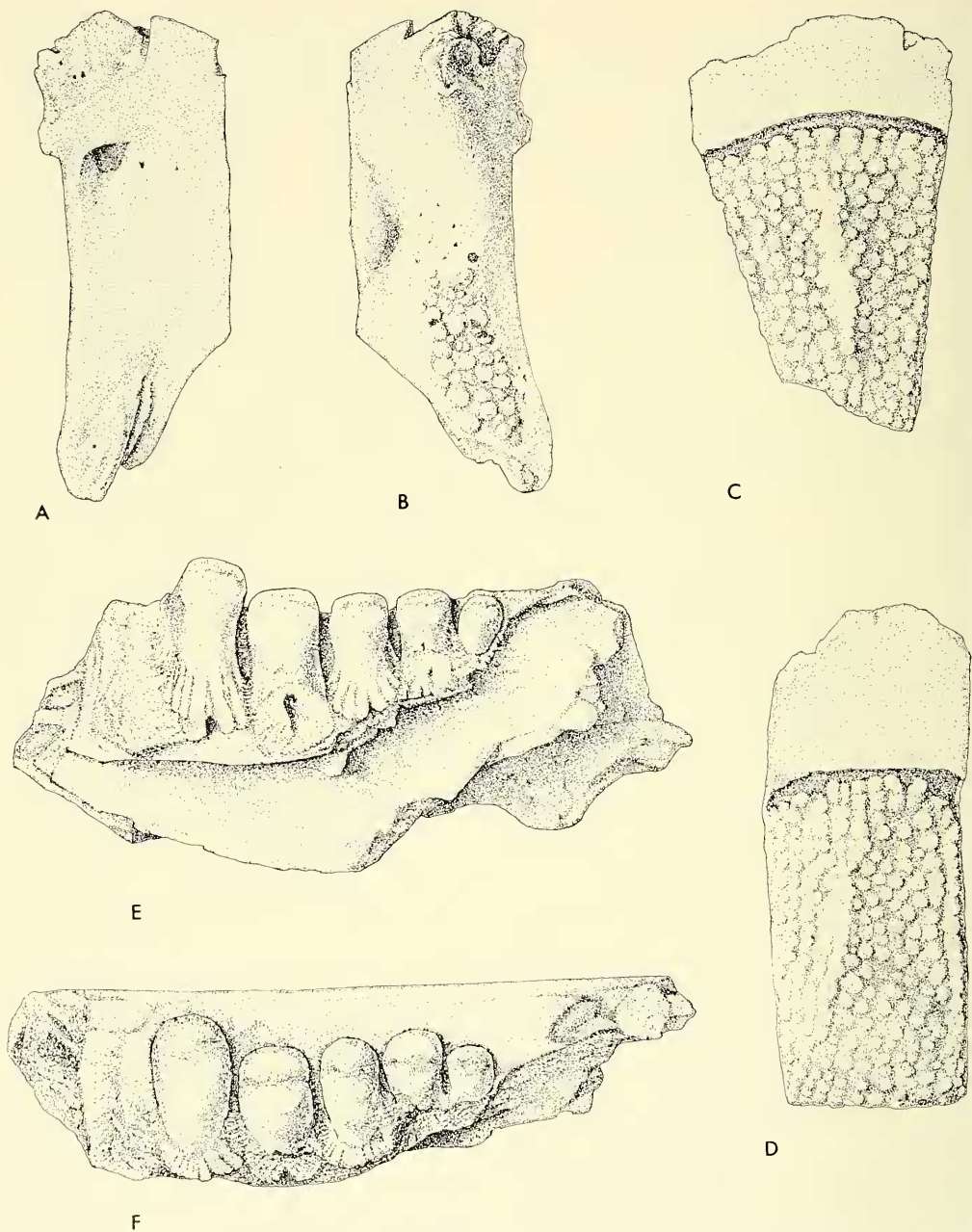
Figure 15. *Arpadosaurus gazinorum*, n. gen., n. sp., USNM 25826, holotype. A, left palatine, dorsal view; B, the same, ventral view; C, medial body osteoscute; D, lateral body osteoscute; E, right dentary fragment, lingual view; F, the same, dorsal view. All × 4. Early Eocene, Wyoming.

area surrounded by the anterior ridges is triangular and contains the parietal fossa close to its posterior apex. The parietal fossa is a vertical pit. The posterior ridges are less prominent than the anterior ones, and merge with the latter at a distance about one-half the total length of the parietal.

The posterior portions of both dentaries are preserved. The right fragment (Fig. 15e-f) contains five teeth, the left only four. The teeth increase in size anteriorly; the most anterior tooth is the largest on both fragments. The teeth are robust crushing teeth with blunt, rounded crowns. In dorsal view the crowns are transversely widened, and have weak, longitudinal cutting edges, from which fine ridges extend at a right angle. The bases of the teeth are expanded and weakly striated. The first, second, and fourth teeth of the right dentary fragment have a basal foramen, and the bases of the latter two are excavated. In the right fragment, the anterior labial coronoid articulation surface ends under the first tooth from the rear; both fragments indicate that on the lingual side the coronoid reached the fourth tooth from the rear.

A small portion of the lower jaw in the articular region includes the jaw articulation surface, which is roughly saddle-shaped and raised anteriorly and posteriorly. Close to the articular facet two foramina occur, one posteromesial and the other anterolateral. The former corresponds to the foramen for the chorda tympani, the latter is the anterior articular foramen.

The greater portion of the right palatine is preserved, with a well-defined patch of tubercular teeth on its ventral surface (Fig. 15a-b). The teeth approach closely, but do not extend as far as, the choana. On the dorsal surface, posterior to the maxillary process, a large, well-defined infraorbital foramen is present. The vomerine process is broken near its base.

The occipital condyle of the occipital region is robust and semi-circular, kidney-shaped in outline. The basi- and exoccipital contributions to the condyle are indistinguishable, as a result of coossification of these bones.

The body osteoscutes (Fig. 15c-d) are longer than wide and covered with the same tubercular mounds as those fused to the frontal and parietal bones. The sculptured surface is separated from the smooth anterior gliding surface by a deep groove. The gliding surface occupies one-third to one-fourth the entire length of the osteoscute. Most of the osteoscutes are rectangular, some with an asymmetrical keel. Other osteoscutes are wedge-shaped, the apex directed posteriad; all of these bear keels. The lateral edges are beveled, and at the same time the irregular surfaces present in this region indicate suturing between adjacent osteoscutes.

Discussion. Arpadosaurus gazinorum is known only by a single specimen from what Gazin (1962) refers to as the La Barge fauna. It is comparable in size to the paratype of *Melanosaurus maximus* and to *Glyptosaurus rugosus*. In the general shape of the frontals, and in having rectangular body osteoscutes that are sutured to one another laterally, *A. gazinorum* also resembles the above genera. However, in a number of characters *A. gazinorum* is intermediate between *Melanosaurus maximus* and *Glyptosaurus rugosus*.

On the ventral surface of the parietal (Fig. 16) the triangular area enclosed by the anterior ridges is largest in *Melanosaurus*, smallest in *G. rugosus*, and intermediate in *A. gazinorum*. These same ridges converge in *G. rugosus* to form a narrow but high mesial ridge. This same mesial ridge is broad and flat in *Melanosaurus;* the anterior ridges continue side by side instead of forming a strong single ridge, as in *G. rugosus.* The situation in *A. gazinorum* is once again intermediate. *Arpadosaurus* resembles *Glyptosaurus* in that the parietal fossa is a vertical pit. *Melanosaurus* has a slanted parietal fossa. The general proportions of the parietal table of the
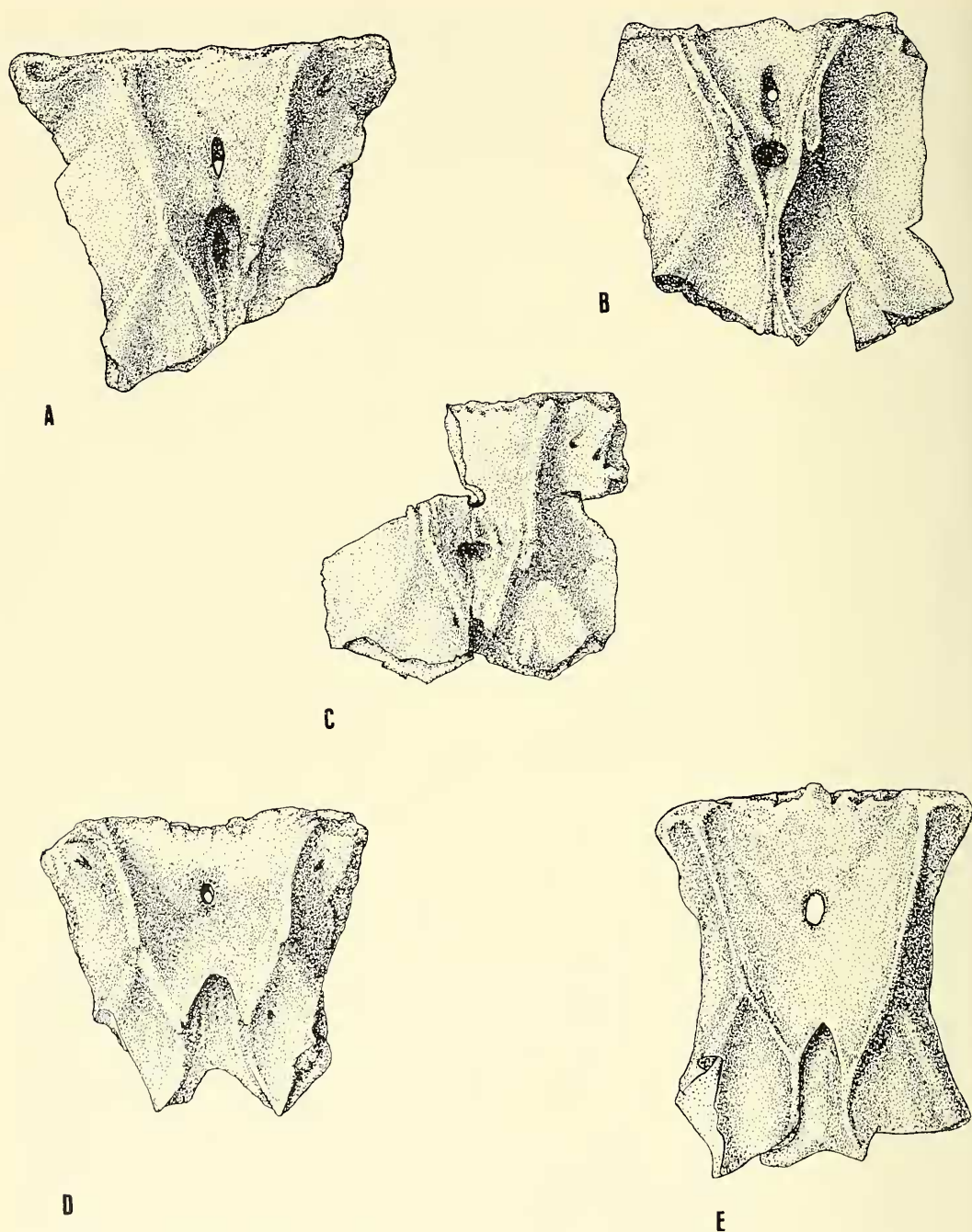
Figure 16.   Parietals of fossil anguids in ventral view. A, *Melanasaurus maximus*, AMNH 5175, paratype, $\times$ 2; B, *Glyptasaurus rugasus*, AMNH 6055, $\times$ 2; C, *Arpadasaurus gazinarum*, n. gen., n. sp., halotype, $\times$ 2; D, *Peltasaurus granulosus*, KU 620, $\times$ 5; E, *Pancelasaurus piger*, n. gen., MCZ 3498, $\times$ 6 (Hell Creek Formation, Montana).

former two genera are also similar. This bone is essentially quadrangular in both of the above, while in *Melanosaurus* the same bone is more elongated.

The scutellation on the dorsal surface of the parietal of *Arpadosaurus* resembles much more that of *Melanosaurus* than of *Glyptosaurus*. In the first two genera, interparietal and occipital impressions are discernable; in *Glyptosaurus* the dorsal surface is covered by subequal polygonal plates.

The osteoscutal crust on the dorsal surface of the frontal bones of *A. gazinorum* is subdivided into unequal epidermal scute areas by numerous grooves; this surface is also irregular, featuring large depressed areas as well as elevated mounds. It is conceivable that further subdivisions of the osteoscutal crust could have led to the situation encountered in *Glyptosaurus*, in which numerous polygonal osteoscutal plates cover the frontal and other cranial bones.

Arpadosaurus gazinorum displays a number of features intermediate between *Melanosaurus* and *Glyptosaurus*, but since it occurs in strata of the same age as *Melanosaurus* and some glyptosaurs, *A. gazinorum* cannot at this time be regarded as anything more than a structural intermediate between the two genera. The origin of glyptosaurs perhaps lay in the Paleocene or very early Eocene.

Glyptosaurus Marsh 1871

Helodermoides Douglass 1903

Type species of the genus. Glyptosaurus sylvestris Marsh 1871.

Referred species. Glyptosaurus nodosus, G. rugosus, G. brevidens, G.? sphenodon, G. princeps, G. hillsi, G. obtusidens, and *G. donohoei* from the Eocene of North America; *G. montanus, G. giganteus,* and *G. tuberculatus* from the Oligocene of North America; *Glyptosaurus* near *nodosus* was recognized by Gilmore (1943) from the Eocene of Mongolia.

Geological range. Early Eocene to Oligocene of North America, Eocene of Mongolia, and questionably Paleocene to Eocene of Europe (see below).

Synopsis of known characters of the genus

The frontals, parietals, and the cheek region are covered by numerous polygonal osteoscutal plates. These cranial osteoscutes, as well as those of the body, are covered with raised tubercular mounds, which are often arranged in concentric patterns. The frontals are distinct or fused; in the latter case the point of fusion is generally marked by a raised ventral ridge. The palatines and pterygoids bear teeth. The postfrontals and prefrontals are narrowly separated above the orbit. The parietal foramen is present, and the postorbital is excluded from orbit formation. The body osteoscutes are rectangular, have a uniform width, and are much longer than wide. They are covered with tubercular mounds that are arranged in a concentric pattern. A deep groove is present between the smooth anterior gliding surface and the sculptured area. The gliding surface is an anterior transverse band and comprises about one-quarter of the total length of the osteoscutes. In every species some of the osteoscutes have feeble keels. Strongly jagged lateral edges indicate suturing between adjacent osteoscutes.

On the mandible the anterior extremities of the coronoid and surangular are in line on a vertical plane on the labial surface. The dentary reaches posteriad between the above two bones to the anterior supraangular foramen (Fig. 17b).

A survey of the glyptosaurs

Numerous polygonal plates sculptured with tubercular mounds cover the cranial elements as well as the cheek region in all the species of *Glyptosaurus*. These individual cranial plates may be rather flat, as in *G. hillsi, G. princeps,* and *G. sylvestris,* or strongly raised, forming a highly irregular

surface, as in *G. donohoei*, *G. giganteus*, *G. nodosus*, *G. rugosus*, and *G. tuberculatus*. These cranial osteoscutes tend to become larger in an anteroposterior direction (e.g. plates covering the parietal are larger than the ones on the frontal, and those covering the cheek region are even larger). The frontals are distinct in *G. sylvestris*, *G. nodosus*, *G. montanus*, and *G. tuberculatus*. These bones are fused but with a prominent suture line or a raised ridge marking the point of fusion, in *G. rugosus*, *G. hillsi*, *G. princeps*, and *G. giganteus*. In the other species the condition of the frontals is not determinable. The parietals are much shortened in *G. giganteus* and *G. montanus* relative to other species where this bone is known. In these same two species the frontals are also foreshortened, and postfrontals and prefrontals closely approach one another over the orbit. In *G. giganteus* the latter two bones are almost touching. In other species of *Glyptosaurus* prefrontals and postfrontals are moderately separated from one another.

Teeth in this genus range from the robust bulbous crushing teeth of *Glyptosaurus hillsi* (similar to the ones described and figured for *Arpadosaurus gazinorum*) to the recurved teeth with pointed unstriated apices of *G. tuberculatus* (similar to those of *Pancelosaurus pawneensis*, Pl. 1). *G.?* *sphenodon* has very slender teeth, and is much smaller than any of the other glyptosaurs; it is probably not a *Glyptosaurus*. The teeth in general are moderately heavy, with obtuse crowns that bear striations and an anteroposteriorly directed cutting edge. The largest members of this genus are *G. hillsi* and *G. giganteus*. The former probably had a slender and elongated head; in the latter the head was broad and relatively short. Both forms exceed by far the maximum size of any other known anguid. *G. nodosus* is the smallest glyptosaur. All species in which the mandible is known display the characteristic labial suturing between dentary and postdentary bones, in which the anterior extremities of the

coronoid and surangular are on a vertical line (Fig. 17b), and the anterior inferior alveolar foramen is between the dentary and the splenial.

Discussion. The glyptosaurs are large lizards, some comparable in size to *Arpadosaurus* and *Melanosaurus*, while some (e.g. *G. giganteus* and *G. hillsi*) are much larger. The glyptosaurs are unique among anguids in that the head osteoscutes are broken up into numerous polygonal plates, resembling superficially in this respect the living *Heloderma*. These small bony osteoscutes are more loosely associated with the skull bones that they cover than is the case in many other anguids and consequently some are often missing. The polygonal plates, as well as the body osteoscutes, are covered with the same tubercular mounds as skull and body osteoscutes of *Melanosaurus*, *Arpadosaurus*, *Peltosaurus granulosus*, and *Xestops vagans*. This type of sculpture is not found in other fossil or Recent members of the Anguidae. The labial contact between the dentary and postdentary bones on the mandible is also nearly identical, in the glyptosaurs, to the latter four fossil genera further indicating that the affinities of glyptosaurs are with these forms. Osteoscutes of glyptosaurs are very similar to those of *Melanosaurus* and *Arpadosaurus* in respect to sculpture. general shape, strong lateral suturing, and in having a deep groove between the gliding surface and the sculptured area. As indicated earlier (p. 141), *Melanosaurus*, *Arpadosaurus*, and *Glyptosaurus*, respectively, can be placed in a structural series that may represent steps in the evolution of glyptosaurs from a more primitive *Melanosaurus*-like ancestor.

Several authors have suggested that the European *Placosaurus* is very close to *Glyptosaurus*, if not congeneric with it, and Romer (1967) lists *Glyptosaurus* as one of the synonyms for *Placosaurus*. Much of what is in the literature at present concerning this question is repetition of assumptions made by early workers. The generic
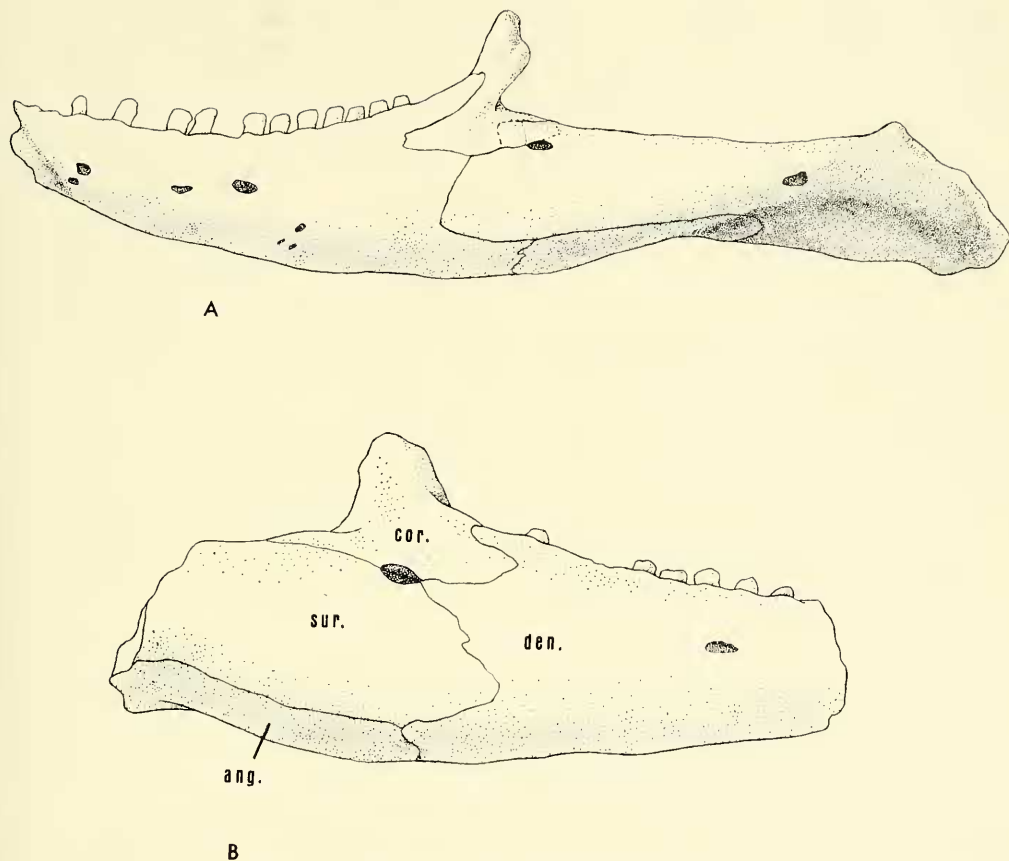
Figure 17. A, left mandible of *Peltosaurus granulosus*, labial view, FAM 42913; B, fragmentary right mandible of *Glyptosaurus*, cf. *G. obtusidens*, AMNH 5176. Note coronoid in advance of surangular in A, the two bones essentially in line in B; A × 3.3, B × 2.7.

name *Glyptosaurus* is retained here for the North American forms until actual study and comparison of the North American and European fossil forms is made.

THE SUBFAMILIES OF ANGUIDAE

The preceding discussion of fossil anguids gives a basis for evaluating the utility of anguid subfamilies based on modern forms. When the fossil record of the group is considered, it is difficult to list a series of characters that characterize the subfamilies, as will be seen below and as has been intimated frequently in the above review.

Anguinae. This group includes *Pancelosaurus*, the most primitive of known fossil anguids, and its limbless modern relatives *Anguis* and *Ophisaurus*. Because of the adaptive differences between the fossil and Recent forms, this subfamily is especially difficult to characterize, but all included forms share unfused frontals with well-separated frontoparietal epidermal scales, and a similar type of scutellation. *Anguis* has somewhat modified its scutes from the *Ophisaurus* condition (Fig. 6); the latter more closely resembles *Pancelosaurus*, gerrhonotines, and glyptosaurines in scute morphology. In the mandible, the sur-

angular and angular extend far forward of the coronoid in the Recent forms, slightly less so in *Pancelosaurus.* A premaxillary foramen is present in the Recent forms and probably, but not certainly, also occurred in *Pancelosaurus.* Vomers, palatines, and pterygoids are toothed in *Ophisaurus,* and at least the latter two bones were toothed in *Pancelosaurus* as well; palatal teeth are absent in *Anguis.*

Pancelosaurus was a limbed form, and was probably ancestral to the glyptosaurines; it also shows strong similarities to diploglossines and to gerrhonotines. It is close to the basal stock of known Anguidae.

Gerrhonotinae. Only the Recent genera *Gerrhonotus, Abronia,* and, perhaps, *Coloptychon* are included. This specialized group has fused, hourglass-shaped frontals, the frontoparietal scales almost or barely in contact on the midline, and lacks the premaxillary foramen of anguines and diploglossines. The forward extension of surangular and angular, and the type of scutellation, suggest that the group is derived from primitive limbed Anguinae.

Glyptosaurinae. This group includes only the extinct genera *Xestops, Peltosaurus, Melanosaurus, Arpadosaurus,* and *Glyptosaurus* (and their European relatives, for which synonymy is not yet clear). This subfamily possesses tuberculated osteoscutes, and the latter three genera show an increasing tendency to fragment the cephalic scutellation. The palate is toothed on palatines, and pterygoids in forms in which these bones are known. The premaxillary foramen is absent in *Peltosaurus,* but the condition in the other genera is not known; this character thus cannot be used to link *Peltosaurus* with the gerrhonotines. On the mandible, labial extensions of coronoid and surangular anteriorly are in a vertical plane except in *Peltosaurus,* which is anomalous in having the coronoid exceed the surangular.

This group is probably derived from *Xestops,* which is differentiated from the anguine *Pancelosaurus* mainly by its tuber-

culated osteoscutes. *Xestops* gave rise, probably, to the Oligocene *Peltosaurus,* in which the frontoparietal scales meet broadly on the midline. *Glyptosaurus,* the most extreme of the group in fragmentation of cephalic scutellation, was probably derived from *Xestops* through *Melanosaurus*-like and *Arpadosaurus*-like ancestors, and it lived through Oligocene time at least.

Diploglossinae. Only the Recent genera *Diploglossus* (including *Celestus* and *Sauresia*), *Ophiodes,* and *Wetmorena* are included here. This primitive group is distinctive, and has no fossil record outside of its present distribution in the West Indies. Cycloid scales with a peaked gliding surface distinguish them from all other anguids, although they are linked to the Anguinae by their separate frontals with well-separated frontoparietal scale impressions.

As might be expected, the fossil record thus shows intergradation between the rather well-defined Recent subfamilial groups. The resemblances of the fossil *Pancelosaurus* are primarily to the Anguinae; nevertheless, strong resemblances to the other subfamilies also occur.

Regardless of the intergradation shown above, the subfamily categories based on Recent forms may be maintained because they appear to represent actual lineages long established in the fossil record. The addition of the Glyptosaurinae is necessary, in addition, to encompass the Eocene-Oligocene radiation of forms with tuberculated osteoscutes.

SUMMARY AND CONCLUSIONS

The foregoing survey of the osteology and epidermal scalation of Recent Anguidae indicates that all extant forms fall into three groups worthy of subfamily status: (1) Anguinae (including *Ophisaurus* and *Anguis*), (2) Gerrhonotinae (including *Abronia, Gerrhonotus,* and possibly *Coloptychon*), (3) Diploglossinae (including *Diploglossus, Wetmorena,* and *Ophiodes*). All these extant forms, excepting the ger-

rhonotines (*Abronia* and *Gerrhonotus*), have paired frontal bones and a premaxillary foramen (see Fig. 2). This foramen is restricted, among Recent lizards, to the genera *Ophisaurus, Anguis, Diploglossus, Wetmorena,* and *Ophiodes.* It may possibly have been present in the fossil genus *Pancelosaurus,* but its presence in other fossil forms cannot be determined except in *Peltosaurus,* in which it is absent. These characters clearly set the Gerrhonotinae apart from the other Recent anguids, but gerrhonotines do share a similar body scutellation and a lateral fold with the ophisaurs. In this respect the Diploglossinae, with their unique (in anguids) cycloid body osteoscutes, stand apart from the rest of the Recent forms.

The anguines, sharing some characters with both, appear to be structurally intermediate between the Gerrhonotinae and the Diploglossinae. They are primitive (except for *Anguis*) in regard to their toothed pterygoids and palatines (and vomers in some), although Recent forms are limbless.

Anguis shares a great number of osteological as well as scalation characters with *Ophisaurus* (see page 101), differing from this genus only in characters judged here to be degenerate: (1) reduced interclavicle; (2) complete absence of palatal teeth; (3) thin, feebly-developed osteoscutes with the anterior gliding surface reduced so as to become confluent with the lateral bevel; (4) absence of a lateral fold, a feature apparently correlated with the reduction of the body armor; (5) absence of an external ear opening (a condition also found in some *Ophisaurus*). *Anguis* appears to be a degenerate ophisaur derived from a limbless *Ophisaurus* ancestor.

In the North American fossil record, fossil remains unquestionably those of lizards of the family Anguidae first occur in late Cretaceous sediments of Wyoming and Montana. This anguid, formerly known as *Peltosaurus piger,* was first described by Gilmore (1928) on the basis of two jaw elements. The generic assignment was based on a tooth structure similar to that of the Oligocene *Peltosaurus granulosus.* This early anguid is here placed in a new genus, *Pancelosaurus,* based on study of a large number of previously unknown cranial elements recovered through washing and screening methods.

The cranial elements of *Pancelosaurus piger,* in their close resemblance to those of some Recent genera (*Ophisaurus, Gerrhonotus, Diploglossus*), point to the fact that most of the Eocene and Oligocene fossil anguids represent a side line of anguid evolution rather than being ancestors of the Recent forms (see below). *Pancelosaurus piger* exhibits a mosaic of characters in its skeleton, showing some resemblance to each of the above Recent genera, especially *Ophisaurus.* Since its body osteoscutes most closely resemble those of *Gerrhonotus* and *Ophisaurus,* perhaps this Cretaceous form was already specialized toward the line leading to these two Recent genera. It exhibits many of the same primitive and intermediate characters between the diploglossines and the gerrhonotines as do the ophisaurs and is regarded here as a primitive limbed member of the Anguinae.

Pancelosaurus piger is known from late Cretaceous through late Paleocene deposits. The genus extends into the middle Oligocene as *P. pawneensis* (formerly *Xestops pawneensis*). *Pancelosaurus* is the only fossil anguid in late Cretaceous and Paleocene deposits of North America that is known to such an extent as to allow for generic diagnosis. *Peltosaurus jepseni,* described by Gilmore, is a synonym of *P. piger.*

The large Eocene and Oligocene fossil forms such as *Xestops, Peltosaurus, Melanosaurus, Arpadosaurus,* and *Glyptosaurus* may also have been derived from *Pancelosaurus* or its relatives, as is indicated by similar body osteoscutes. These are more robust than those of *P. piger* and contrast with those of the latter in being covered

with tubercular mounds. This sculpture type is found only in the above Eocene and Oligocene forms, and combined with a characteristic pattern of labial suturing between dentary and postdentary bones, indicates their distinctness from other anguids. They are placed here in the extinct subfamily Glyptosaurinae. In this concept of the glyptosaurines, the Eocene species *Xestops vagans* appears to be the most primitive form, sharing some primitive characters of the frontal bones with *P. piger*, while exhibiting the above-mentioned glyptosaurine characters. *Dimetopisaurus wyomingensis* is a synonym of *Xestops vagans*.

All the known North American genera referable to the Glyptosaurinae occur in deposits only of Eocene (*Arpadosaurus, Glyptosaurus, Melanosaurus,* and *Xestops*) or Oligocene (*Glyptosaurus* and *Peltosaurus*) age. However, three large, keeled body osteoscutes bearing the diagnostic tubercular sculpture of the Glyptosaurinae have been reported by Estes and Tihen (1964) from the Mio-Pliocene Valentine Formation of Nebraska. Unless they are reworked, these scutes indicate that some unknown glyptosaurine survived until the late Miocene or early Pliocene.

In the Glyptosaurinae, the new genus *Arpadosaurus* appears to be structurally intermediate between *Melanosaurus* and *Glyptosaurus,* and it is postulated that the glyptosaurs may have originated from a form like *Melanosaurus;* more evidence is needed to confirm this hypothesis, however.

It is postulated above that *Pancelosaurus piger* or a closely related form may have given rise to both the extant ophisaurs and gerrhonotines or only to the former. There is indeed nothing in the known anatomy of *P. piger* that would contradict such an assumption, but in the absence of a more complete fossil record, the origin of these Recent forms is still hypothetical.

The only fossil form referred to the Gerrhonotinae and consisting of more than

jaw elements is *Paragerrhonotus ricardensis* (Estes, 1964) from the early Pliocene of California. This fossil form poses more problems than it solves. Although frontal bones are fused and display strongly emarginate concave borders as in the Recent *Gerrhonotus,* the osteoscutal crust on the frontal is broken up into several facets instead of exhibiting the usual epidermal imprints of Recent anguids. This is a trend often seen in anguimorphs (cf. *Parasaniwa, Glyptosaurus, Exostinus, Heloderma*). It is probably a specialized sideline, derived from *Gerrhonotus.*

Estes (1964) regarded some anguid dentaries from the Lance Formation as near *Gerrhonotus.* These jaw fragments with *Gerrhonotus*-like teeth occur in the same deposits as *Pancelosaurus piger.* No other cranial elements have been recovered. Without the presence of the specialized frontals of *Gerrhonotus* (or a closely allied form) in the Cretaceous, its presence cannot be confirmed, and it is also possible that these jaw fragments may represent a smaller species of *Pancelosaurus.*

Gerrhonotus-like jaws were also noted by McKenna (1960) from the Eocene (Wasatchian) Four Mile local fauna of Colorado, and the Mio-Pliocene Valentine Formation of Nebraska (Estes and Tihen, 1964). These identifications, like those from the Lance Formation, are not supported so far by any other cranial elements.

Remains of ophisaurs referable to or close to Recent species have been described both from the Pliocene of Europe and from the Pleistocene and Pliocene of North America, and Mlynarski (1960, 1964) described the remains of *Ophisaurus pannonicus* from the early Pliocene of Poland. He regarded this form as very close to if not conspecific with *Ophisaurus apodus.* From these same deposits Mlynarski (1964) described the remains of *Anguis* cf. *fragilis.* Etheridge (1960) recognized the extant *O. attenuatus* as early as the late Pliocene of Kansas. Auffenberg (1955) recognized both *O. ventralis* and *O. compressus* from

the Pleistocene of Florida. Thus it appears that establishment of the Recent species of *Ophisaurus* had begun at least by the beginning of the Pliocene, and that *Anguis* was distinct from the ophisaurs by that time.

The middle Eocene European Geiseltal deposits contain numerous anguid fossils; some were said by Kuhn (1940) to show resemblance to the ophisaurs. I have not seen this material, and Kuhn's figures are poor, but study of this material will shed some more light on the phylogeny of the Anguinae as here constituted, as well as on that of the Anguidae in general.

The diploglossines have no fossil record beyond Pleistocene cave finds (Etheridge, 1964, 1965).

The preceding account illustrates the incomplete state of the fossil record of the Anguidae, especially that of the Recent forms, and also the need for new discoveries, as well as reworking of existing fossil material.

Some of the main conclusions reached by this investigation may be summarized as follows:

(1) The Recent anguids and the North American fossil forms fall into four groups worthy of subfamily status: (1) Anguinae, (2) Diploglossinae, (3) Gerrhonotinae, (4) Glyptosaurinae. The Diploglossinae, in many ways primitive, has essentially no fossil record; the Glyptosaurinae is extinct.

(2) The Glyptosaurinae (*s.l.*) contains most of the well-known fossil anguids (*Glyptosaurus, Melanosaurus, Peltosaurus,* and *Xestops*) and a new genus, *Arpadosaurus.*

(3) The glyptosaurines appear in the early Eocene of North America and disappear from the fossil record by or just before the beginning of the Pliocene.

(4) *Peltosaurus,* long considered a close relative of *Gerrhonotus,* is shown to have a greater resemblance to the glyptosaurines (especially *Xestops*).

(5) The earliest known anguid is *Pan-celosaurus piger* from the late Cretaceous of Wyoming and Montana. This is the only anguid fossil in Cretaceous and Paleocene deposits of North America that is known to such an extent as to allow generic diagnosis. A related species, *P. pawneensis,* occurs in the Oligocene of Wyoming.

(6) *Pancelosaurus piger* displays a body scutellation similar to that of *Gerrhonotus* and *Ophisaurus,* and this early fossil appears to be already a member of the Anguinae, but the imperfect fossil record prevents more positive statements concerning the phylogeny of the above Recent forms.

Abbreviations

a = angular
aaf = anterior inferior alveolar foramen
ain = anterior internasal epidermal scale
amf = anterior mylohyoid foramen
asf = anterior supra-angular foramen
c = coronoid
d = dentary
e = ectopterygoid
fn = frontonasal epidermal scale
fp = frontoparietal epidermal scale
fr = frontal epidermal scale
ip = interparietal epidermal scale
m = maxilla
oc = occipital epidermal scale
pa = parietal epidermal scale
part = fused articular and prearticular
pf = premaxillary foramen
pfr = prefrontal epidermal scale
pin = posterior internasal scale
pl = palatine
pm = premaxilla
pt = pterygoid
r = rostral epidermal scale
sa = surangular
so = supra-orbital epidermal scale
sp = splenial
v = vomer

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